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A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands

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Abstract. Salinization, a widespread threat to the structure and ecological functioning of inland and coastal wetlands, is currently occurring at an unprecedented rate and geographic scale. The causes of salinization are diverse and include alterations to freshwater flows, land-clearance, irrigation, disposal of wastewater effluent, sea level rise, storm surges, and applications of de-icing salts. Climate change and anthropogenic modifications to the hydrologic cycle are expected to further increase the extent and severity of wetland salinization. Salinization alters the fundamental physicochemical nature of the soil-water environment, increasing ionic concentrations and altering chemical equilibria and mineral solubility. Increased concentrations of solutes, especially sulfate, alter the biogeochemical cycling of major elements including carbon, nitrogen, phosphorus, sulfur, iron, and silica. The effects of salinization on wetland biogeochemistry typically include decreased inorganic nitrogen removal (with implications for water quality and climate regulation), decreased carbon storage (with implications for climate regulation and wetland accretion), and increased generation of toxic sulfides (with implications for nutrient cycling and the health/functioning of wetland biota). Indeed, increased salt and sulfide concentrations induce physiological stress in wetland biota and ultimately can result in large shifts in wetland communities and their associated ecosystem functions. The productivity and composition of freshwater species assemblages will be highly altered, and there is a high potential for the disruption of existing interspecific interactions. Although there is a wealth of information on how salinization impacts individual ecosystem components, relatively few studies have addressed the complex and often non-linear feedbacks that determine ecosystem-scale responses or considered how wetland salinization will affect landscape-level processes. Although the salinization of wetlands may be unavoidable in many cases, these systems may also prove to be a fertile testing ground for broader ecological theories including (but not limited to): investigations into alternative stable states and tipping points, trophic cascades, disturbance-recovery processes, and the role of historical events and landscape context in driving community response to disturbance.

Key words: biodiversity; biogeochemistry; ecosystem services; global change; hydrology; wetland; non-linear feedbacks; salinization; salinification; saltwater intrusion.

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INTRODUCTION

Throughout human history, anthropogenic manipulations of the hydrologic cycle have artificially altered the balance of salt and water on the landscape leading to increased salinity in some wetlands, inland aquatic systems, and upland soils. This accumulation of soluble salts, which causes ionic concentrations to increase above natural levels, is known as salinization. Today, wetland salinization is occurring at an unprecedented geographic scale and at rates that far exceed natural changes in salinity, with profound consequences for wetland and aquatic systems (Williams 1999, 2001, Bailey et al. 2006, Cañedo-Argüelles et al. 2013). Interactions between global climate change and anthropogenic alterations of the hydrologic cycle are likely to further increase the incidence and severity of wetland salinization in the coming decades (Neubauer and Craft 2009). Wetland salinization has the potential to degrade wetlands, alter ecosystem-level processes and landscape dynamics, impact the valuable ecosystem services provided by wetlands, and, ultimately, feedback to global climate systems.

Wetlands play a critical role in providing freshwater, improving water quality, sequestering carbon, regulating climate, mitigating storm surges, and supporting biodiversity (Costanza et al. 1998, Zedler 2003, Zedler and Kercher 2005, Barbier et al. 2011). Despite the ecological importance of wetlands and the magnitude of the salinization threat, there is no up-to-date assessment of wetland salinization on a global scale. Recent research indicates that many wetlands undergoing salinization display unique, non-linear behavior indicative of rapid, and perhaps irreversible, environmental change (Davis et al. 2003, Strehlow et al. 2005, Sim et al. 2006, Davis et al. 2010, Larsen et al. 2010, Runyan and D'Odorico 2010), suggesting that comparisons between freshwater and saline wetlands (Redeke 1922, Remane 1934, Remane and Schlieper 1971, Odum 1988, Hopkinson et al. 1999, Craft 2007, Wieski et al. 2010) may not be

the best model for understanding wetland salinization. On a global scale, the extent of wetland salinization is poorly quantified. Existing literature on wetland salinization is geographically limited (Bailey et al. 2006) and often restricted to comparisons of hydrogeomorphically similar wetlands or modes of salinization (Findlay and Kelly 2011). Furthermore, existing studies of salinization commonly focus on single ecosystem processes or individual biological components (e.g., microbial metabolism, plant community composition). Such narrow approaches do not take into account the complex indirect, non-linear feedbacks that may control state changes in wetland ecosystems (Bridgman et al. 2008, Larsen et al. 2010, Neubauer et al. 2013, Hopfensperger et al. 2014).

To better understand how salinization affects freshwater wetlands, we present the following global synthesis of the ecological impacts of wetland salinization. Our goals are to (1) establish a common vocabulary to aid scientists working across disciplines and within different types of ecosystems, (2) summarize the causal mechanisms and potential geographic extent of salinization, (3) synthesize the current understanding of the multi-scale effects of salinization on wetland structure and function, emphasizing common underlying drivers across systems, and (4) highlight emerging gaps in our knowledge as to how salinization will affect wetland ecosystems. Throughout this review, we will draw examples and inferences from the literature on both coastal (tidal) and inland freshwater wetlands, contrasting the two wetland types when the consequences of salinization are likely to be significantly different.

DEFINING UNITS AND TERMINOLOGY

Salinization has occurred throughout the Earth's history via the natural accumulation of salts; this process is known as *primary salinization*. Throughout geologic time, the salinity of inland and coastal water bodies has varied considerably in response to glacial/interglacial cycles and

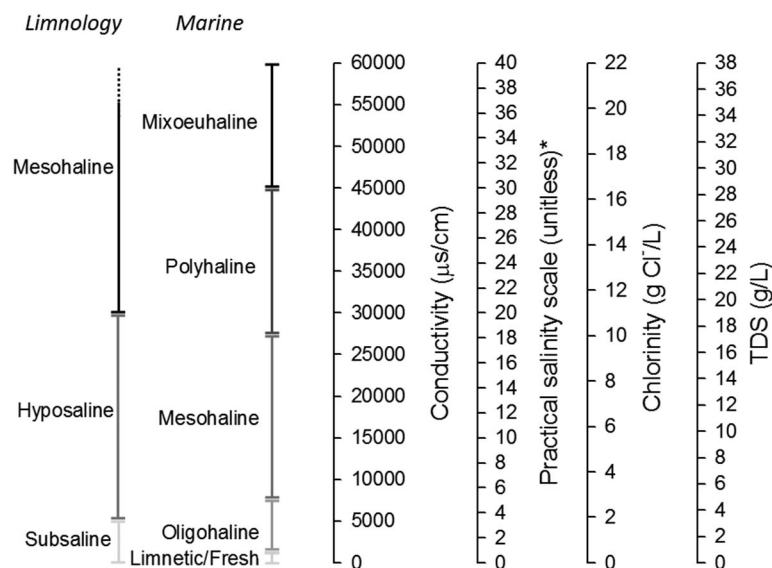


Fig. 1. Common terms used in limnologic and marine fields for the classification of saline ecosystems and the various measurements of salinity used in these fields. This Fig. is provided so that the reader may approximate conversions across studies. These relationships are valid for aquatic media with ionic compositions similar to diluted seawater, and vary with ionic composition, temperature, and ionic strength. Salinity is presented as measures of conductivity ($\mu\text{S/cm}$), practical salinity units (*psu; also equivalent to parts per thousand or ppt), chlorinity ($\text{g Cl}^-/\text{L}$), and total dissolved solids (TDS; g/L) and their relative scales at 25°C . Equations for conversion are from Dauphinee (1980), Lewis (1980), and Close (1990).

associated changes in continental water, sea level, and temperatures. Associated changes in salinity occur over a time scale of approximately 100,000 years, though further variation arises over shorter orbital cycles of 23,000 to 41,000 years (Pages 2k Consortium 2013, Neukom et al. 2014). In contrast, increases in salt concentrations caused by anthropogenic forces are known as *secondary salinization*. Secondary salinization can occur on a time-scales as short as decades, and in some cases even more rapidly. Human alterations of the hydrologic balance of landscapes will interact with natural hydrologic variation leading to accelerated salinization in many parts of the world. Throughout this review, we will refer to secondary salinization alone, or in combination with natural salinizing processes in wetlands, simply as *salinization*. In the literature, the process of salinization is sometimes called salinification or seawater/saltwater intrusion or incursion.

There is little agreement regarding the meanings of the terms *fresh* and *saline* among different

practitioners (see Williams 1987; Fig. 1). In inland aquatic systems, salinity is measured as chloride (Cl^-) content ($\text{g Cl}^-/\text{L}$) or total dissolved solids (TDS, g/L ; Fig. 1). Electrical conductivity (EC, $\mu\text{S/cm}$) is often used as a proxy for TDS. In marine systems, salinity is measured on the practical salinity scale (PSS) as the ratio of the conductivity of a sample to that of a reference (Lewis 1980). Although this metric of salinity is unitless, it is often expressed as practical salinity units (psu). Throughout this review, salinities are generally reported using the units of the original publications, except where a direct comparison across studies is paramount. Where it was necessary to convert between units, we used the formulae provided in Dauphinee (1980), Lewis (1980), and Close (1990). These relationships are valid for aquatic media with ionic compositions similar to seawater (Table 1), but do vary with ionic composition, temperature, and ionic strength. Fig. 1 is provided so that the reader may approximate conversions.

Table 1. Select examples of the elemental composition of fresh and saline waters provided for comparison of ionic concentrations and variation in ionic ratios. Total dissolved solids (TDS) and ion concentrations are reported in mg/L; ionic ratios are molar.

Water	TDS	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	Cl ⁻	SO ₄ ²⁻	Fe	SO ₄ ²⁻ /Cl ⁻
Precipitation									
Sewen (France)†		0.1	0.0	0.3	0.2	0.6	1.4		0.9
Mexico City (Mexico)‡		1.4	0.1				6.4		
Freshwater river									
Mean river water§	120	15	4.1	6.3	2.3	7.8	11	0.7	0.5
Pristine river (Q ₉₉)¶	2,314	186.4	71.7	333.4	19.7	602.7	696		0.4
Pristine river (Q ₁)¶	4.8	0.6	0.1	0.4	0.2	0.1	0.2		0.7
Seawater (35 psu)#	35,169	412	1,284	10,781	399	19,353	2,712	0.01	0.1
Arid rivers									
Murray River (Australia)	262.8	15	12	50	4.8	78	21		0.1
Yamuna River (India)††	287	31.8	9.6	32.2	5.1	41.5	39.6		0.3
Tigris, (Iraq)‡‡	437	64.5	21.7	47.7		82.6	66.5		0.3
Wastewaters									
Gas well brine (USA)§§	157,000	11,200	875	36,400	281	98,300	<50	47	
Coal-mine effluent (USA)¶¶	6,468	237	53.7	1,952	25.1	792	3,672	0.44	3.0
Agricultural drain (USA)##	14,400	0.4	242	3.72	3.1	1210	8,350		2.5
Saline groundwater									
Sudbury Basin, (Canada)	1,295	155	74	36	11.7	26	768	9	10.8
New S. Wales (Australia)†††	1,882	43.9	255	154.7	2.2	327.3	782.3	6.5	0.9
Timna aquifer (Israel)‡‡‡	14,157	2770	24	2350	18	8180	717		0.0

†Sanusi et al. 1996, ‡Báez et al. 2007, §Langmuir et al. 1997, ¶Meybeck 2003, #Pilson 2012, ||Herczeg et al. 1993, ††Sarin and Krishnaswami 1984, ‡‡Mutlak et al. 1980, §§Haluszczak et al. 2013, ¶¶Kennedy et al. 2005, ##Kharaka et al. 1996, |||Frape and Fritz 1982, †††Jankowski and Acworth 1997, ‡‡‡Vengosh and Rosenthal 1994.

CAUSES AND EXTENT OF SALINIZATION IN FRESHWATER WETLANDS

The mechanisms of salinization are diverse and vary according to a given wetland's climatic and geomorphic setting, and the type and extent of anthropogenic forcing. Throughout this manuscript, we introduce select case studies illustrative of these diverse causes, but refer the reader to Fig. 2 and Table 2 for a more extensive account of documented cases of salinization. The overall consequence of the convergence of human modifications of hydrology and global climate change will be not only increased salinity in freshwater wetlands and underlying aquifers but also more variable salinity regimes. While some causes of salinization are thoroughly discussed in the literature (e.g., dryland salinization in inland Australia, saltwater intrusion into coastal estuaries), salinization has yet to be assessed in many settings and its true geographic extent is unknown. In this section, we identify distinct salinization mechanisms and the settings in which they occur to highlight the potential for wetland salinization across geographic and geomorphic settings.

Salinization of inland wetlands

Salinization of inland wetlands occurs when salts are mobilized by surface or groundwater movement and concentrated in the soils of floodplain or depressional freshwater settings. We have identified five mechanisms that can contribute to the secondary salinization of inland freshwater wetlands: (1) vegetation clearance, (2) intensive irrigation, (3) river regulation, (4) mining and extraction, and (5) de-icing salts, all of which may be intensified by global climate change. The first three mechanisms are confined largely to Mediterranean, arid, and semi-arid landscapes (Table 2). The fourth and fifth mechanisms occur across wide geographic ranges, and selected case studies are identified in Table 2.

The first two mechanisms apply in areas that lie over shallow, naturally saline aquifers. Firstly, the clearance, *en masse*, of deep-rooted, perennial vegetation (grasses, shrubs, and trees) decreases evapotranspiration and disrupts pre-existing hydrological conditions resulting in elevated saline water tables and an upward movement of water and salt through the soil profile (Macumber 1990, Eamus et al. 2006). Evapotranspiration further concentrates salts at the soil surface. This process is commonly known as

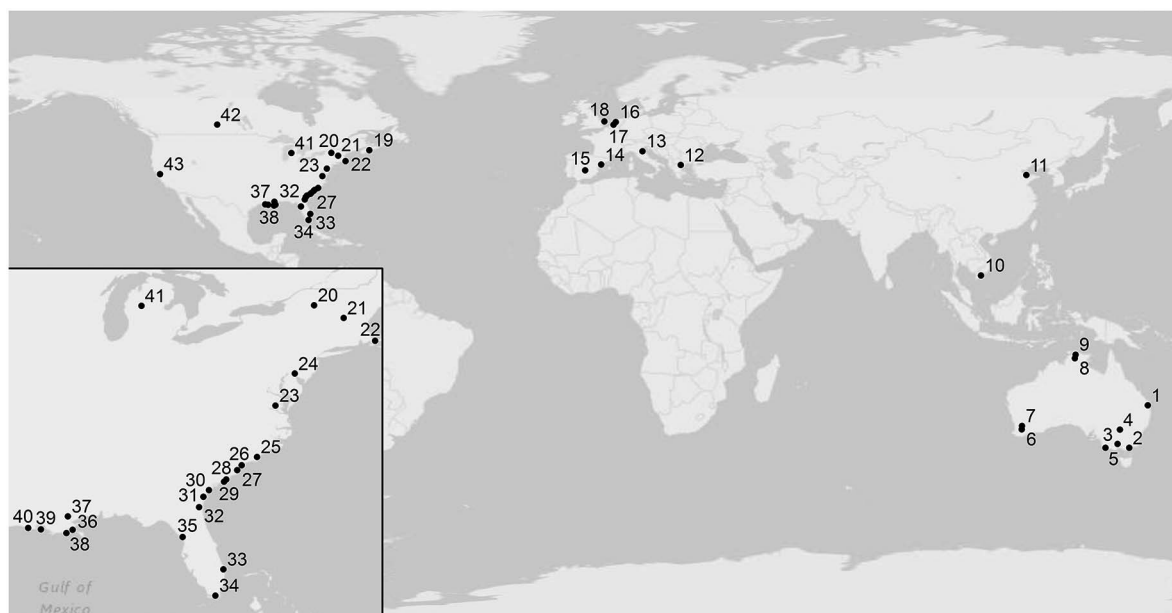


Fig. 2. Distribution of documented cases of freshwater wetland salinization. Each numbered location is identified and described in Table 2. The absence of data from large geographic areas of the world does not imply the absence of wetland salinization. While we may assume wetland salinization is occurring at a much broader scale concomitant with the salinization of land and soil resources, we present only cases reported in primary literature. We did not include laboratory, mesocosm, or experimental manipulations.

dryland salinization, because it occurs in landscapes that are not irrigated. The second mechanism results when the application of excessive amounts of irrigation water causes saline groundwater to rise (Smedema and Shiati 2002). In both cases, capillary action can draw saline water to the surface even when the water table remains as deep as two meters from the surface (Eamus et al. 2006).

Human-induced movement of saline groundwater has resulted in the salinization of soils across the world (Ghassemi et al. 1995, Schofield et al. 2001, Mazi et al. 2014). Even in regions without shallow saline groundwater, the surface or groundwater used to irrigate crops is invariably more saline than rainwater. High rates of evapotranspiration result in increased soil salt loads over time (Nosetto et al. 2008). Salts may be flushed into wetland areas during natural precipitation events, in dust plumes, or during the disposal of high-salinity spent irrigation waters that result from periodic flushing of salts from agricultural soils (Ghassemi et al. 1995, Williams 2001). Climate change driven warming and shifts

in the magnitude and variability of precipitation along with population growth are estimated to increase irrigation demands globally (Vörösmarty et al. 2000, Döll 2002, Fischer et al. 2007), exacerbating irrigation-driven salinization.

The third mechanism, river regulation, primarily affects floodplain wetlands by modifying the natural patterns of wetting and drying and increasing the frequency or duration of dry-down. The chronic desiccation of wetlands, for example, decreases hydrostatic head, allowing saline groundwater to penetrate the bed of the now-dry wetland, resulting in rapid salinization (Jolly et al. 2008, Boon et al. 2009, Crosbie et al. 2009). Modern-day land clearing, irrigation, and river regulation go hand-in-hand in agricultural landscapes, and it is often difficult to separate the individual effects of these disturbances. Globally, population growth and climate change are projected to increase relative water demand (a measure of demand per unit discharge, Vörösmarty et al. 2000), increasing the vulnerability of floodplain wetlands.

The interaction of these various mechanisms in

Table 2. Cases of wetland salinization recorded in the literature.

Map #	Site	Location	Mechanism	Reference
1	Mary River	Queensland, Australia	Sea level rise	Knighton et al. 1991
2	Gippsland Lakes	Victoria, Australia	Artificial maritime navigation channel, reduction in freshwater riverine inputs	Bird 1961, 1962, 1966; Boon et al. 2008; Raulings et al. 2010, 2011; Wheeler et al. 2010
3	Central Victoria	Australia	Vegetation clearance, dryland salinity, irrigation elevating saline water tables	Hart et al. 1990
4	Murray-Darling Basin	New South Wales, Queensland, and South Australia	Vegetation clearance, irrigation raises saline groundwater	Walker 1985; Walker et al. 1993; Walker and Thoms 1993
5	Piccaninnie Ponds	South Australia	Sea level driven intrusion of saltwater into aquifer with subsequent discharge into groundwater-fed wetland	Wood and Harrington 2014
6	Toolibin Lake	South-western Australia	Saline runoff, elevated saline groundwater	Drake et al. 2014
7	Wheatbelt region	South-western Australia	Vegetation clearance, dryland salinity, irrigation elevating saline water tables, evapoconcentration	Goodsell 1990; Halse et al. 2003
8	Kakadu National Park	Northern Territory, Australia	Tectonic subsidence, SLR, changes in fluvial geomorphology	Winn et al. 2006; Sandiford 2007
9	Alligator River	Northern Australia	Climate variability, SLR	Nelson et al. 2015
10	Mekong River Delta	Vietnam	Storm, discharge variation, river channel modifications	Wassmann et al. 2004
11	Yellow River Delta	China	Decreased freshwater flows	Cui et al. 2009
12	Axios River delta	Greece	Seasonal saltwater intrusion due to low river flow; water diversion for irrigation	Zalidis 1998
13	Revano River	Ravenna, Italy	Draining associated saltwater intrusion, progressive groundwater salinization, strong storm events	Antonellini and Mollema 2010
14	Ebro River Delta	Spain	Water management reduces freshwater flows	Prat and Ibañez 1995
15	Tablas de Daimiel National Park	Spain	Water management, groundwater pumping, drought	Berzas et al. 2000
16	North Holland	The Netherlands	Salinization of groundwater due to lowland reclamation and sea level rise	Essink 2001
17	Haringvliet Lake	The Netherlands	Restoration of estuarine conditions (seawater re-intrusion into current freshwater lake)	Canavan et al. 2006
18	River Thurne catchment	Norfolk, United Kingdom	Wetland draining and subsequent intrusion of seawater into aquifers	Holman and Hiscock 1998
19	Nova Scotia	Canada	Road salt accumulation	Collins and Russell 2009
20	Adirondack Mountains	New York, USA	Road salt accumulation	Karraker et al. 2010
21	Northern States	USA	Road salt accumulation	Kaushal et al. 2005; Findlay and Kelly 2011
22	Cape Cod	Massachusetts, USA	Dike breaching	Portnoy and Gibling 1997a, 1997b; Portnoy 1999; Smith et al. 2009
23	Delaware River	Delaware, USA	Seasonal saltwater intrusion due to low river flow	Weston et al. 2014
24	Pamunkey River	Virginia, USA	Seasonal saltwater intrusion due to low river flow	Neubauer and Anderson 2003
25	Cape Fear estuary	North Carolina, USA	Channel widening and deepening increased tidal range, sea level rise	Hackney and Yelverton 1990
26	Waccamaw River	South Carolina, USA	Decreased freshwater flow due to water regulation (reservoirs), sea level rise, Hurricane surge	Blood et al. 1991; Michener et al. 1997; Conrads and Roehl 2007; Noe et al. 2013

Table 2. Continued.

Map #	Site	Location	Mechanism	Reference
27	Hobcaw Barony	South Carolina, USA	Hydrologic alteration associated with abandoning agricultural impoundments and culvert instillation, drought, Sea level rise	Krauss and Duberstein 2010
28	Albemarle Peninsula	Tyrell County, North Carolina, USA	Microtidal system with wind-driven tides, droughts, higher rate of sea level rise than global averages	Ardón et al. 2013; Manda et al. 2013; Helton et al. 2014; Hopfensperger et al. 2014
29	Kiawah Island	Charleston, South Carolina, USA	Dike construction, coastal freshwater pond receives salt-water influx during storm events	Aelion and Warttinger 2009, 2010
30	Savannah River	Georgia, USA	Channel alteration, sea level rise, multi-year drought	Wetzel et al. 2004; Krauss et al. 2012
31	South Newport River	Georgia, USA	Upstream hydrologic alteration	Jun et al. 2012
32	Satilla River	Georgia, USA	Drought	Meiggs and Tallefert 2011
33	Loxahatchee River	Florida, USA	Reduced freshwater flow	Kaplan et al. 2010
34	Taylor Slough, Everglades National Park	Florida USA	Canal construction, water management, decreased freshwater flows	Lorenz 2014
35	Turtle Creek, Waccasassa Bay State Preserve	Florida, USA	Sea level rise	Williams et al. 1999
36	Mississippi River Delta	Louisiana, USA	Hurricane surge, oil/gas exploration and transport canals	Penfound and Hathaway 1938; Chabreck and Palmisano 1973; Wang 1988; Guntenspergen et al. 1995
37	Lake Pontchartrain, Madisonville	Louisiana, USA	Sea-level rise	Baldwin and Mendelssohn 1998
38	Terrebonne and Barataria Basins	Louisiana, USA	Hurricane surge	Jackson et al. 1995
39	Marsh Island Wild Life Refuge	Louisiana, USA	Hurricane surge	Geddes and Mopper 2006
40	Rockefeller State Wildlife Refuge	Grand Chenier, Louisiana, USA	Oligohaline marsh expansion in the last 60 years; Dredging of north-south waterways, occurrence of large-scale muskrat (<i>Ondatra zibethica</i>) eat-outs, and a severe drought	Bolduc and Afton 2003
41	Osceola and Crawford County	Michigan, USA	Road salt accumulation	Blasius and Merritt 2002
42	St. Denis	Saskatchewan, Canada	Climate variability	Nachshon et al. 2013
43	San Francisco Bay-Delta	California, USA	Freshwater diversions, channelization, drought	Williams 1989; CCW District 2010; Enright and Culberson 2010

Note: Laboratory, mesocosm, or experimental manipulations are not included.

initiating landscape-scale salinization is evident strongly in the Murray-Darling Basin of eastern Australia (Fig. 2, Table 2). The Basin covers 14% of the Australian landmass and much is underlain by a shallow saline aquifer of marine origin. The clearance of nearly two-thirds of the trees, and almost all of the deep-rooted perennial grasses, combined with intensive irrigation and the associated water extraction and river regulation, resulted in rising saline groundwater

(Walker et al. 1993). This is compounded by the impoundment of the rivers of the region, including the three largest: the Darling, the Murray and the Murrumbidgee, by 248 large dams, which has altered the timing and reduced the magnitude of freshwater discharge downstream (Finlayson et al. 2013). Such severe alterations to natural hydrological cycles have resulted in secondary salinization across the Basin and continue to be responsible for exten-

sive degradation of wetlands, floodplains, and rivers (e.g., see Walker 1985, Walker et al. 1993, Jolly et al. 2001, Mac Nally et al. 2011, Pittock and Finlayson 2011). The Basin has been identified as a model of much of the planet's future with regard to water shortages, environmental degradation, and climate change (Pittock and Connell 2010).

The fourth mechanism of salinization of inland freshwater wetlands occurs as a consequence of mining and other industries that discharge saline wastewater into aquatic systems. For example, the extraction of oil via traditional technologies produces waste brine when a naturally saline groundwater formation is encountered during drilling or when brine is used for secondary oil recovery (Newport 1977, Vengosh et al. 2014). In the Marcellus shale region of the United States, the salinity of these formations ranges from 25 to ~250 g TDS/L. In most regions, the storage and disposal of these saline wastewaters is highly regulated, but leaks, spills, and illegal direct discharges have led to observed increases in soil and surface water salinity (Vengosh et al. 2014). Although long ignored as a causative mechanism, this process will become increasingly important as efforts are made to extend fossil-fuel resources by the extraction of coal-seam gas and shale oil (Rogers et al. 2011, Lutz et al. 2013). Surface-water fed wetlands are especially at risk.

A second example of salinization due to wastewater discharge is in the Alberta oil sands region of Canada. Surface strip mining for bitumen exposes marine sediments and shallow saline aquifers, resulting in salinization due to dumping of saline mine overburden, increased discharge of deep saline groundwater at the surface, and the disposal of saline waters used in the extraction of oil from the sands (Kessler et al. 2010, Gibson et al. 2013). These processes have been predicted to modify salinity regimes in boreal wetland ecosystems (Trites and Bayley 2009). While many mining activities expose marine groundwater formations, others expose solid minerals that are dissolved and carried into aquatic systems by precipitation. Stockpiles of salts used in the manufacture of potash fertilizers leach potassium (K^+), sodium (Na^+) and Cl^- while surface coal mining results in effluent high primarily in sulfate (SO_4^{2-} ; Cañedo-Argüelles et al. 2013). The effects of mining activities on

surface water salinity are well documented (see review by Cañedo-Argüelles et al. 2013), but the extent to which this salinity accumulates in inland wetlands has not been assessed. Wetlands are poised on the landscape to intercept salinized surface flows as well as intersect salinized groundwater. Furthermore, potability restrictions drive salinity regulation in flowing waters (Cañedo-Argüelles et al. 2013), but inland wetlands are generally not subject to these regulations.

The fifth mechanism that we identified, the application of de-icing road and airport salts, is a form of salinization that is limited to northern latitudes (Turnbull and Bevan 1995, Koryak et al. 1998, Kaushal et al. 2005). Aircraft de-icing agents contain glycol- and potassium salts, and are known to overspray or drip onto impervious surfaces or be dispersed onto the airfield only to be washed into nearby waterways (Switzenbaum et al. 2001). A medium-sized airport may use over 1000 m³ of airplane de-icing agents over a winter season (Betts 1999). Road salts, primarily NaCl (although salts of magnesium and calcium [e.g., $MgCl_2$ and $CaCl_2$] are also used), can be transported into adjacent aquatic ecosystems (Karraker et al. 2010). These salts are not flushed as rapidly as surface water, resulting in retention of salt within wetlands and streams (Findlay and Kelly 2011). Kaushal et al. (2005) showed that in the northeastern United States, a highly urbanized area with high densities of roads and other impervious surfaces, Cl^- concentrations are increasing at a regional scale toward thresholds for some freshwater aquatic species, with mean annual Cl concentrations in excess of 0.3 g Cl^- /L. Salts applied in the winter accumulate and concentrate throughout the year, sometimes reaching peak concentrations during summer when biological activity is high (Findlay and Kelly 2011). De-icing salts are currently the most inexpensive method for road de-icing and their use is projected to increase in the coming decades as impervious surface cover expands (Kaushal et al. 2005, Findlay and Kelly 2011). While evapoconcentration itself is a natural (primary) mechanism for salinization, increasing global temperatures will enhance the evapoconcentration of road and other salts in inland wetlands experiencing secondary salinization.

Salinization of coastal wetlands

Seawater intrusion, incursion, or inundation is the movement of marine waters into historically freshwater wetlands via surface or subsurface flow. Coastal freshwater wetlands exist along the estuarine continuum with downstream brackish and salt marshes, where tide range, prevailing winds, river discharge, and local geomorphology determine salinity distributions. Coastal wetlands are sensitive to changes in marine processes and freshwater flows from upstream catchments. We identify five mechanisms of salinization in coastal wetlands, including: (1) surface or subsurface seawater intrusion linked to sea level rise (SLR), (2) reductions of riverine freshwater flow, (3) alterations of subsurface freshwater, (4) anthropogenic alteration of coastal geomorphology, and (5) storm surges. Salinization via many of these mechanisms is likely to be accelerated due to regional and global climate changes.

The first mechanism of salinization of coastal freshwater wetlands is surface or subsurface seawater intrusion due to sea level rise (SLR). Sea level rise alters hydrologic gradients and pushes seawater further inland. Low-lying coastal wetlands are particularly sensitive to SLR (Park et al. 1989, Eliot et al. 1999). Sea level fluctuations have also been observed to push saline water into inland groundwater-fed wetlands via movement of the subterranean freshwater-saltwater interface (Wood and Harrington 2014). Sea level rise in coastal areas has already resulted in the intrusion of marine waters into previously freshwater wetlands (Table 2), and this trend is expected to accelerate over time as rates of SLR increase from current rates of 2.2–3.6 mm yr⁻¹ (Church and White 2011), to as much as 15.6 mm yr⁻¹ by 2100 (Church et al. 2013). As a consequence of global climate change, mean sea level is projected to increase by 0.19–0.83 m by 2100 (Church et al. 2013) with some models projecting increases of more than 1 m by 2100 (Richardson et al. 2009, Vermeer and Rahmstorf 2009, Rignot et al. 2011). Sea level rise does not manifest as a smooth, linear increase; rather, SLR rates vary over time and between regions, complicating predictions for saltwater intrusion. For instance, SLR rates in the Pacific are dampened during negative phases of the Pacific Decadal Oscillation, and positive phases will

accelerate SLR (NRC 2012). A similar effect of the 18.6-year lunar nodal cycle is also observed (Baart et al. 2011).

The contribution of SLR to coastal wetland salinization varies geographically, as there is great spatial variation in regional trends of relative SLR due to smaller-scale variation in water temperature, surface winds, and geologic activity (Church et al. 2013, Rhein et al. 2013). In the Kakadu region of Northern Australia, a combination of tectonic subsidence and recent eustatic SLR has resulted in seawater intrusion (Sandiford 2007). As a result, there has been a 9-fold increase in the area of bare saline mudflats in the East Alligator River region of Northern Australia (Fig. 2, Table 2) since the 1950s, and a 64% decrease in the area of freshwater wetlands (Winn et al. 2006).

The second mechanism responsible for secondary salinization of coastal wetlands is the reduction of riverine freshwater flows debouching into coastal embayments or estuaries, which will compound changes in estuarine salinity gradients due to SLR (e.g., Fluin et al. 2007). Reduced freshwater flows alter hydrologic gradients, allowing saltwater to penetrate further upstream. Climate change is predicted to alter the magnitude and timing of precipitation and thus freshwater discharge (Nijssen et al. 2001). In some parts of the world, climate change may increase freshwater availability and therefore decrease wetland salinity, but this is beyond the scope of this review. Anthropogenic activity has also directly altered freshwater discharge through the construction of dams and diversion of freshwater for municipal, industrial, and agricultural uses (Newport 1977, Prat and Ibañez 1995, Montagna et al. 2002). Many of the largest rivers in the world have experienced declines in freshwater flows due to extraction and regulation, almost always involving the construction of large dams or serial weirs (Stanley and Warne 1993). The net result of these structures has been the upstream progression of the tidal wedge, facilitating the inundation of previously freshwater systems with saline waters.

The San Francisco Bay-Delta (California, USA) is a prime example of how both natural and anthropogenically mediated fluctuations in river discharge can alter the distribution of salinity (Fig. 2, Table 2). One of the largest water

development projects in the world annually withdraws as much as 70% of the freshwater flows of the rivers of the Bay-Delta (Holmes 2012), which has altered the hydrologic gradient, pulling saltwater into previously freshwater areas (Williams 1989, CCW District 2010, Enright and Culberson 2010). The catchment is also projected to receive lower overall precipitation, and a lower proportion as snowfall, resulting in high winter flows and reduced spring and summer flows, allowing further seawater intrusion at ecologically important times of the year (Parker et al. 2012).

The third mechanism responsible for salinization of coastal freshwater wetlands relates to changes in groundwater recharge and discharge. Like surface water, groundwater in coastal zones is sensitive to extraction-mediated salinization. The extraction of freshwater from coastal aquifers alters subsurface hydrologic gradients, salinizing aquifers and, subsequently, overlying wetlands (Waterkeyn et al. 2008, Barlow and Reichard 2010, Ferguson and Gleeson 2012, Mazi et al. 2014).

Anthropogenic manipulations of coastal geomorphology, the fourth mechanism of salinization in coastal wetlands, principally affects coastal floodplain wetlands. One example of this process is in the widespread dredging employed to deepen existing channels for deepwater navigation, which results in the upstream movement of seawater in many rivers (e.g., Newport 1977, Hackney and Yelverton 1990, Keddy et al. 2007, Krauss et al. 2012). In the coastal zone of the Netherlands, for example, the combination of lowland reclamation in the past centuries and ongoing SLR is expected to lead to strong salinization this century (Essink 2001). In the Savannah River (Georgia/South Carolina, USA; Fig. 2, Table 2), multiple channel deepening projects have resulted in seawater intrusion (Duberstein and Kitchens 2007). Similar impacts are expected due to dredging of deepwater channels in the Yangtze and Pearl River Deltas of China (Zhang et al. 2011, 2012).

Channels excavated for navigation, water conveyance, and pest control in sinuous estuarine river systems result in more efficient movement of saltwater into previously freshwater systems (Day et al. 2007, Manda et al. 2014). For example, numerous navigation channels were excavated in the Mississippi River Delta

(Louisiana, USA). These channels have been implicated in increased salinities throughout the Delta as well as increased peak salinities associated with hurricane surges (Day et al. 2007). The Gippsland Lakes, on the south-eastern coast of Australia, were opened to the Southern Ocean in 1889 resulting in the lakes transitioning from an intermittently open and closed freshwater lagoon system to an estuarine system within a few decades (Bird 1966, Bird and Rosengren 1971). The salinization of this system has been further exacerbated by freshwater diversions from the inflowing rivers for irrigation, industrial, and municipal use (Wheeler et al. 2010). Artificial coastal freshwater impoundments constructed for agriculture, wildlife habitat, and pest control (Montague et al. 1987) are also at risk from salinization. Breaching impoundments (intentionally or unintentionally) results in rapid salinization, altering soil and water chemistry (Portnoy and Giblin 1997*a, b*, Portnoy 1999, Smith et al. 2009) and, although these systems represent small land areas, they have been important in the study of wetland salinization (Table 2).

The fifth mechanism, storm surges, can introduce saline water into coastal freshwater wetlands along the estuarine continuum, and in near-shore lagoons and depressional wetlands that have no permanent hydrologic connection to the sea (Fig. 2, Table 2). Hurricanes, and other tropical storms and storm-associated tidal surges, are expected to increase in frequency and intensity over the coming century (Mousavi et al. 2011, Schuerch et al. 2013), which will affect local systems sporadically and unpredictably. Rhein et al. (2013) report that the average height of 50-year flood events has increased 2–10 cm/decade since 1970, indicating saltwater may penetrate further inland and upstream in the future. Although tsunamis lead to direct salinization of groundwater and soil in coastal areas, normal salinities may be restored within a year as a result of monsoon rains (Kume et al. 2009). In combination with droughts or low soil permeability, the effects of marine inundation are expected to last longer.

THE GLOBAL EXTENT OF SALINIZATION

The secondary salinization of previously fresh inland and coastal wetlands is a worldwide

ecological problem (Fig. 2, Table 2). However, assessing the global extent of wetland salinization is difficult, as few governments have allocated the resources needed to quantify the problem. Ghassemi et al. (1995) undertook a global assessment of land and water salinization, with a focus on agricultural production. They concluded that worldwide, more than 76×10^6 ha of land was salt-affected. More recently, Wicke et al. (2011) estimated that, globally, 1.1×10^9 ha of land was salt-affected and 14% (1.5×10^8 ha) of this area is classified as forest, wetlands, or other legally protected area. Given that wetlands cover only $5.3\text{--}12.8 \times 10^8$ ha globally (Zedler and Kercher 2005), these numbers suggest a substantial portion of wetlands may be salt affected. Although the above figures are not necessarily representative of the extent of inland freshwater wetland salinization, they hint at the broad extent to which wetland salinization may be occurring. Wetland ecosystems are found at lower elevations, intercepting surface water or in close proximity to (or intersecting) groundwater tables, and thus are predicted to salinize more rapidly than nearby uplands (Jolly et al. 2008).

Similarly, outside of the individual cases recorded in the literature (Fig. 2, Table 2), coastal wetland salinization has not been quantified. In a recent World Bank report regarding the susceptibility of wetlands in developing countries to SLR, Blankespoor et al. (2012) projected that freshwater wetlands would be lost at an average rate of 64% to submergence and conversion to saline systems following a 1-m rise in sea level, with the highest regional loss rates in the Middle East and North Africa (100%), Latin America and the Caribbean (74%), Sub-Saharan Africa (72.5%), and East Asia and the Pacific (62.2%). Henman and Poulter (2008) estimated that, worldwide, there were approximately 15×10^6 ha of coastal wetlands below 5-m elevation, and thus vulnerable to projected SLR. The Australian and New Zealand Environmental and Conservation Council predicts significantly elevated salt concentrations in 40,000 km of their waterways and associated wetlands by 2050 (Nielsen et al. 2003). Although there are no specific estimates regarding current or future freshwater wetland salinization in inland and coastal systems, it is clearly a global problem that is likely to get worse. While it is logical to assume that wetland

salinization is occurring in regions where (upland) soil and water salinization is occurring, documentation of wetland salinization is rare. While the above studies suggest salinization of water and soil resources are occurring globally, our review of the literature shows that documented cases of wetland salinization appear to be concentrated in three areas: Australia, Europe, and the Atlantic coast of the United States. Documenting the salinization of wetland resources is the first step in assessing the potential for ecosystem degradation.

ENVIRONMENTAL EFFECTS OF SALINIZATION

Increased salinity exerts effects on freshwater wetlands in a number of ways (Williams 2001, Bailey et al. 2006). Increased ionic concentrations rapidly alter the abiotic environment, leading to profound changes in sedimentation and sediment chemistry. Saline water carries with it many ions that can alter the dynamics of inorganic chemical interactions, change the predominant biogeochemical reactions (Fig. 3A), and shift microbial communities that drive elemental cycles. Many of the economically valuable ecosystem functions of freshwater wetlands, such as their ability to sequester carbon (C) or phosphorus (P) and remove nitrogen (N) from floodwaters, are markedly altered by salinization (Fig. 3A, B). In organisms, salinization disrupts the uptake of water and essential ions by the presence of high external concentrations of solutes, and induces direct toxic impacts on individual organisms arising from the accumulation of ions in cells leading to mortality (Kozłowski 1997). Salinity can exert ecological impacts in a wide range of other, indirect or non-lethal, ways, altering productivity, species distributions, and community interactions (Fig. 3B). In this section we discuss both the direct and indirect impacts of salinization on individual ecosystems components and the potential ramifications for the important ecosystem services provided by wetlands.

Because freshwater biota is affected by both the composition and concentration of dissolved ions (Table 1), and the frequency and duration of exposure to elevated ionic concentrations (Nielsen et al. 2003), it is important to consider these factors when assessing the impacts of salinity.

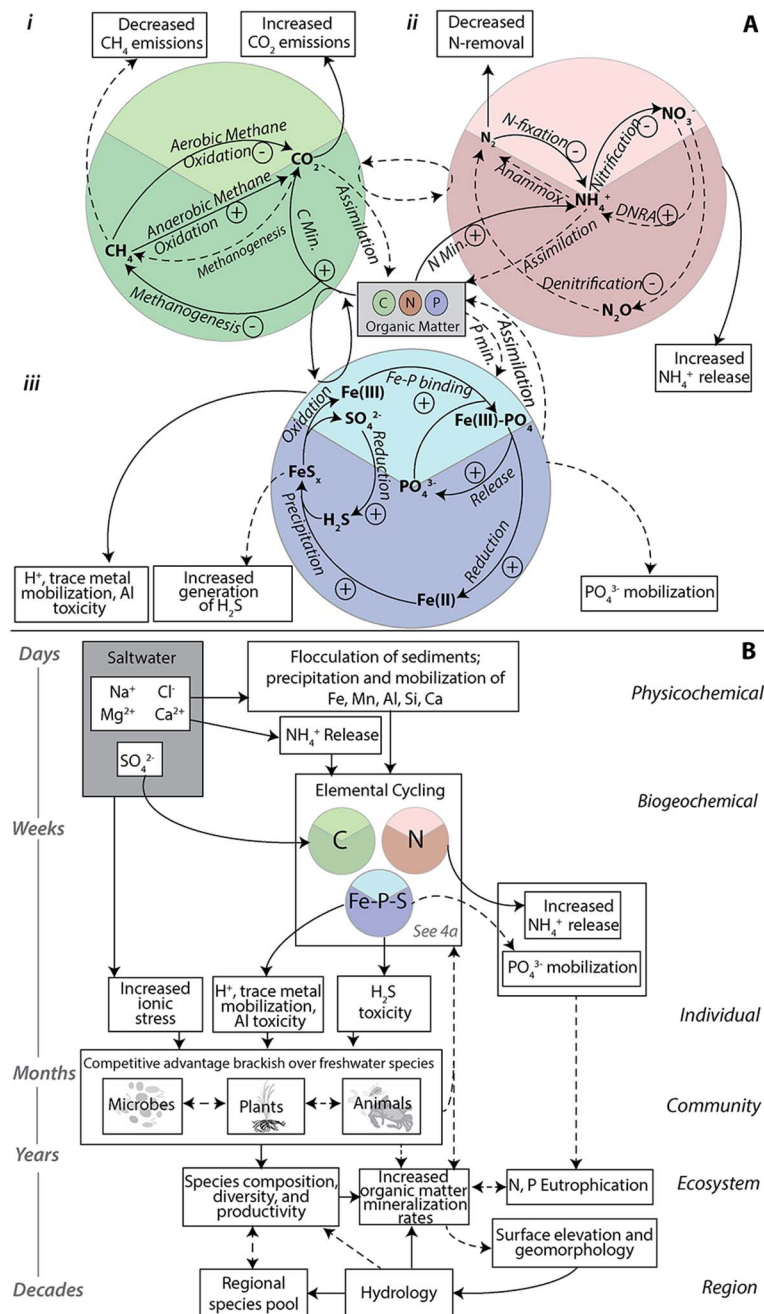


Fig. 3. Conceptual diagram of the predicted changes in freshwater ecosystems as they undergo salinization. (A) Predicted changes in biogeochemical cycling in freshwater wetlands. Changes in both aerobic (light 1/3 of each circle) and anaerobic (dark 2/3 of each circle) biogeochemistry of (i) carbon, (ii) nitrogen and (iii) iron-phosphorus-sulfur cycling are described. Arrows are indicative of biogeochemical transformations predicted to increases (+) or decrease (–) in response to salinization. Solid arrows indicate pathways for which there is a high degree consensus for the expected direction of change, while dashed lines indicate pathways for which there is little research or conflicting predictions regarding the expected direction of change based on our literature review. For those pathways with an extremely high degree of uncertainty regarding the expected outcome, no direction

(continuation of Fig. 3 legend)

(+ or -) is presented. The expected net outcome of biogeochemical change due to saltwater intrusion are represented in boxes. (B) Predicted ecosystem effects of salinization. Saltwater constituents (grey box) alter multiple ecosystem components from physicochemical changes to the abiotic environment to regional pools of species over multiple time scales. Solid arrows indicate pathways for which there is a high degree of consensus for the expected direction of change, while dashed lines indicate pathways for which there is little research or conflicting predictions regarding the expected direction of change. Details of changes in elemental cycling are found in (A).

Salinization can occur on many time scales: it can be a gradual, prolonged, irreversible change (e.g., due to SLR or saline groundwater) or can occur in shorter, periodic pulses (e.g., due to storm surges or seasonal drought). The rates and duration of salinization can have major implications for the alteration of wetland ecosystem processes. Salinization increases soluble salt concentrations, but the specific composition and concentration of total dissolved solids can vary geographically depending on the source of saline water (Nielsen et al. 2003; Table 1). There is considerable spatial variability in the ionic composition of natural saline waters (e.g., seawater vs. arid river), plus large differences between natural waters and salt-rich effluents produced by human activities (Table 1). In coastal regions, salinized systems will reflect the relatively consistent ionic composition of seawater with elevated Na^+ , Ca^{2+} , Mg^{2+} , Cl^- , sulfate (SO_4^{2-}), and bicarbonate (HCO_3^-), while inland systems will reflect variable sources including local groundwater, wastewater effluent, or geologic formations (Table 1). While some of the observed effects of salinization are consequences of specific ions, others are consequences of general osmotic stress. Understanding the source and timing of salinization is essential in predicting its impacts, thus when possible, we have discussed time-scale and ionic composition (Table 1) independently.

Ionic changes in salinizing wetlands

The most immediate consequence of salinization is increased ionic concentration in the soil and overlying water, which alters chemical equilibria and mineral solubility on a short time scale of days to weeks (Fig. 3B). Elevated ionic concentrations reduce the solubility of gases (Stumm and Morgan 1996), resulting in shallower O_2 penetration into the soil profile and more

negative redox potential. Reduced gas solubility also has the potential to accelerate gas emissions and allow less time for internal processing of gases (e.g., CH_4 oxidation, N_2O reduction; see *Biogeochemical Cycling* below). Saline water is denser than fresh water, and saltwater intrusion via surface or groundwater movement can result in the establishment of strong stratification (and the formation of a halocline) in tidal rivers and depressional wetlands (Nielsen et al. 2003), which is a barrier for the movement of O_2 between the freshwater strata and the saline strata below (Legović et al. 1991). Salt loads of merely 2 g/L are enough to alter the density of water enough to produce stratification similar to the temperature-derived, density stratification observed in holomictic freshwater lakes (Findlay and Kelly 2011).

Divalent cations in saltwater (e.g., Ca^{2+} and Mg^{2+}) aggregate suspended matter resulting in the flocculation of sediment (Fig. 3B; Sholkovitz 1976, Grace et al. 1997). Enhanced flocculation increases water clarity in inland systems (Davis et al. 2003), but results in continuously elevated turbidity in estuarine systems where the estuarine turbidity maximum establishes at the saltwater front (de Nijs and Pietrzak 2012). Increased conductivity may also cause hydrophobic soil colloids to repel, reducing hydraulic conductivity and reducing gas and solute transportation through waterlogged wetland soils (Brady and Weil 2004).

Increased ionic strength also alters chemical equilibria by altering thermodynamic activity coefficients and displacing, or blocking, ions from ion exchange sites in the soil matrix (Seitzinger et al. 1991, Stumm and Morgan 1996). Increased concentrations of alkaline earth cations enhance the dissolution of quartz minerals by promoting the hydrolysis of the Si-O bond (Dove and Elston 1992, Dove 1999), increasing

dissolved SiO_3^{2-} concentrations. Sodium and Cl^- can increase the dissolution of Fe and manganese (Mn) minerals due to decreased activity coefficients (Baldwin et al. 2006).

Ionic displacement has been suggested as a mechanism for desorption of many chemical species from salinizing wetland soils, particularly inorganic nitrogen (e.g., ammonium, NH_4^+) and phosphorus (e.g., orthophosphate, PO_4^{3-}) species, with potential consequences for downstream eutrophication. The sediments of freshwater wetlands generally have higher concentrations of exchangeable NH_4^+ than their saline counterparts (Seitzinger et al. 1991) and salinization has been widely observed to mobilize NH_4^+ within hours (Weston et al. 2006, 2010, Findlay and Kelly 2011, Ardón et al. 2013, Jun et al. 2013). Ionic displacement of NH_4^+ is due to increased competition for exchange sites with saltwater cations (Seitzinger et al. 1991) and increased ion pairing with saltwater anions (Gardner et al. 1991). Ammonium release occurs at low salinity (~ 3 psu) and increases with salinity and the number of saline pulses (Weston et al. 2010, Ardón et al. 2013, Jun et al. 2013), although prolonged/permanent salinization may deplete NH_4^+ depending on its concentration at exchange sites (Ardón et al. 2013, Noe et al. 2013). Alternating between fresh and saline conditions may result in repeated pulses of NH_4^+ (Weston et al. 2010).

Inorganic phosphorus (PO_4^{3-}) retention in soils is controlled mostly by cation exchange with clays and organic matter and co-precipitation with metal cations of Fe, Ca, Al and Mg (Richardson 1985, Reddy 1991), all of which can be disrupted by increased ionic content. Many studies have observed increased P release from salinized soils (Portnoy and Giblin 1997b, Lamers et al. 2001, 2002, Weston et al. 2006), while others have observed increased P sorption (Jun et al. 2013), or no change in P (Lamers et al. 2002). Overall, increased ionic strength decreases the activity coefficient of PO_4^{3-} , increasing the solubility of mineral-bound P. However, increased concentrations of ions that bind PO_4^{3-} (e.g., Fe and Ca^{2+}) can precipitate displaced PO_4^{3-} (Baldwin et al. 2006, van Diggelen et al. 2014). Sulfate may also displace PO_4^{3-} from soil exchange sites (Roden and Edmonds 1997, Bruland and DeMent 2009), but this seems unlikely

as PO_4^{3-} has a higher affinity for exchange sites at circumneutral pH (Schachtschabel and Scheffer 1976). As discussed below in *Sulfur, iron, and phosphorus*, increased SO_4^{2-} concentrations can affect rates of sulfate reduction and the stability of Fe-P minerals.

It is clear that salinization can alter the physicochemical nature of the soil environment by altering ionic strength, soil texture, redox state, gas and solute transport, pH, and interfering with multiple elemental cycles. Increased ionic strength alters these processes rapidly, between days and weeks from the onset of salinization, with profound consequences for water quality and the availability of important nutrients for biota. Although the alteration of some processes is consistent across sites, others are highly variable between sites with differing soil characteristics and dissolved ionic constituents.

Biogeochemical cycling

Freshwater wetlands are hotspots for biogeochemical transformations on the landscape (Fig. 3A). Compared with saltwater wetlands, freshwater systems are typically dominated by a different set of biotic and abiotic biogeochemical reactions and this, along with their lower ionic content, high productivity, and high biological activity, imparts their important climate regulation and water quality improvement functions. Denitrification is generally an important pathway for N removal in these systems (Fig. 3A–ii). Nitrogen and P are also sequestered through exchanges on soil surfaces or are bound in organic matter. Frequently, catabolism in freshwater wetlands is dominated by Fe reduction in mineral soils or methanogenesis in organic soils. Thus, in addition to serving as significant sinks for C, many freshwater wetlands contribute to the global C budget by serving as significant sources of CH_4 , a potent greenhouse gas.

The alteration of water chemistry due to salinization changes chemical substrate availability, concentration, and equilibrium, shifting the dominant biogeochemical processes within a wetland and ultimately altering the ability of wetlands to provide key ecosystem services (Fig. 3B). Microbes mediate many biogeochemical transformations in which electrons are shuttled from an electron donor (e.g., organic com-

pounds) to a terminal electron acceptor (TEA) through a complex set of reduction-oxidation (redox) reactions, resulting in free energy that is used to drive metabolic processes. The oxidized and reduced chemical species produced through these redox reactions can undergo abiotic transformations or can be used in other metabolic reactions by different members of the microbial community. While we have some understanding of how elemental cycles work in purely marine or freshwaters, we know much less about how these elemental cycles operate as a system undergoes a transition from freshwater to saline (Day et al. 2008, Craft et al. 2009). Below, we discuss potential changes in biogeochemistry and their implications for salinization of wetland ecosystems.

Sulfur, iron and phosphorus cycling (Fig. 3A–iii).—Sulfur cycling is tightly coupled to Fe cycling, both of which are driven by biotic and abiotic reactions (Einsele 1936, Smolders et al. 2006, Burgin et al. 2011). Under relatively oxic conditions, S and Fe occur in their oxidized forms: SO_4^{2-} and Fe(III)-oxides. These oxidized forms are reduced to sulfide (S^{2-}) and Fe(II) by anaerobic microbial metabolism. Despite SO_4^{2-} concentrations being orders of magnitude lower in freshwaters compared to marine ecosystems (Capone and Kiene 1988), there is strong evidence that SO_4^{2-} reduction can be an important pathway in some freshwater wetland soils (Lovley and Klug 1983, Ingvorsen and Jørgensen 1984, Pester et al. 2012, Segarra et al. 2013). Increasing SO_4^{2-} concentrations are generally associated with rapid increases in SO_4^{2-} reduction rates and the acceleration of overall organic matter mineralization in freshwater wetland soils (Lamers et al. 1998, Weston et al. 2006). Sulfate reduction results in the formation of sulfide (H_2S , HS^- , S^{2-}), which is toxic to many organisms (Lamers et al. 2013).

Microbial Fe(III) reduction can be a dominant C mineralization pathway in both freshwater (Roden and Wetzel 1996, Neubauer et al. 2005b) and saline wetlands (Kostka et al. 2002, Hyun et al. 2007). In laboratory sediment incubations, Weston et al. (2006) observed a short-term (several day) increase in rates of Fe(III) reduction following seawater intrusion attributed to the increased ionic strength and decreased pH. Moreover, salinization itself can introduce new

Fe to the system via influx of Fe-rich saline groundwater (Table 1) or enhanced sediment deposition (see *Ionic effects*). Meiggs and Taillefert (2011) showed that saltwater intrusion into riverine freshwater wetlands resulted in seasonally-enhanced Fe(III) reduction, as a direct result of ion-mediated enhanced mineral deposition. Although Fe reduction is important in regulating microbial C cycling (Neubauer et al. 2005b) the process is rarely assessed in salinizing wetlands.

Reduced sulfur (e.g., H_2S) and iron [Fe(II)] combine abiotically to form iron monosulfide (FeS) and, eventually, pyrite (FeS_2 ; Rickard and Morse 2005, Tobias and Neubauer 2009). Salinization generally increases the concentration of Fe-S minerals in wetland soils (Schoepfer et al. 2014). Iron can act as a “buffer” against the buildup of reduced S compounds in the porewater and related toxicity (van der Welle et al. 2006, Schoepfer et al. 2014). The formation of FeS_x , however, will depend strongly on soil composition and Fe availability. Lamers et al. (2001, 2002) showed differential response of soils to increased SO_4^{2-} wherein systems with high organic matter (electron donor) levels have elevated H_2S concentrations, while in systems rich in Fe, S was pyritized, leading to FeS_x formation and little buildup of porewater H_2S . The relationship between salinity, C availability and the fraction of the total Fe pool bound with S, known as the *degree of sulfidization*, can be used to predict the buildup of H_2S in salinizing soils (Wijsman et al. 2001, Morse et al. 2007, Schoepfer et al. 2014) and gauge potential H_2S toxicity (see *Wetland biota*).

The formation of FeS_x retains S in sediments, which can have other deleterious consequences. Anaerobic soils with high concentrations of FeS_x are often described as potential acid sulfate soils. During dry periods, FeS_x minerals react with O_2 to produce Fe(II), SO_4^{2-} , and acidity (H^+ ; White et al. 1997, Wilson et al. 1999). This leads to acidification, deoxygenation, and the liberation of aluminum (Al) and heavy metals (Johnston et al. 2003, Baldwin and Fraser 2009, Lamers et al. 2014); this cascade highlights the importance of interactions between the hydrologic cycle and the outcome of salinization. Few studies of salinizing environments, particularly wetlands, measure both the Fe and S soil pools and rates of FeS_x mineral formation. Understanding these coupled cycles will be critical to predicting the timing of

wetland transformation in coastal and inland systems experiencing increased SO_4^{2-} concentrations (Lamers et al. 2001, 2002, Schoepfer et al. 2014).

The interaction between S and Fe cycling plays a major role in P cycling. The reduction of Fe(III) to ferrous iron [Fe(II)] and complexation with sulfide results in the dissolution of Fe- PO_4 minerals, and release of PO_4^{3-} (Reddy and DeLaune 2008). Iron-sulfur complexation releases P for weeks to months following saltwater intrusion, which may contribute to the eutrophication of overlying and downstream waters (Lamers et al. 2001, 2002, Weston et al. 2006). There are, however, mechanisms by which salinization can increase P removal. Increased microbial activity associated with Fe(III) and SO_4^{2-} reduction can increase alkalinity, pH, and anion exchange capacity, increasing dissolved Al and Fe concentrations (Portnoy and Giblin 1997b). Additionally, saline waters have high concentrations of Ca^{2+} and Mg^{2+} , and salinization promotes the mobilization of the ions from soil adsorption sites. Neither Ca^{2+} or Mg^{2+} form metal sulfides but both can complex with P (Reddy and DeLaune 2008, Jun et al. 2013, van Diggelen et al. 2014). Prolonged aerobic conditions that arise from changes in hydrology can increase Fe(II) oxidation (see above) and thus can sequester P. For example, in a recent mesocosm experiment, van Diggelen et al. (2014) showed that even in FeS_x -rich sediments, Fe oxidized at the aerobic sediment-water interface was sufficient to trap P and prevent diffusion of P from the sediments.

It is obvious that Fe, S, and P dynamics are highly complex and driven largely by abiotic factors such as water chemistry, soil type, hydrology and other highly site-specific factors. The increased potential for H_2S buildup and subsequent toxicity, and for PO_4^{3-} release, have implications for overall ecosystem health and downstream eutrophication, though these effects may not be apparent with short-term salinization.

Nitrogen cycling (Fig. 3A–ii).—One of the best recognized ecosystem services of wetlands is their ability to ameliorate water quality by retaining N via sorption and incorporation into biomass, and by removing N via denitrification, thus reducing N loads flowing into rivers, lakes

and streams (Costanza et al. 1998, Zedler 2003). The N cycle is dominated by microbial transformations (Fig. 3A–ii), many of which have heretofore been poorly quantified in wetland systems. The dominant paradigm in wetland ecology is that wetlands with more marine characteristics tend to release similar amounts of N, as NH_4^+ and N_2 (via coupled nitrification-denitrification), while freshwater wetlands are dominated by N_2 release (Joye and Hollibaugh 1995) and therefore are more efficient sinks for N.

In anaerobic wetland environments, NH_4^+ dominates the inorganic N pool. It is well established that ionic displacement of NH_4^+ (see *Ionic Effects*) mobilizes N rapidly after salinization. In addition, NH_4^+ is released during the microbial mineralization of organic matter. Salinity is negatively correlated with N in estuarine soils, which has been attributed to a lower rate of decomposition and N mineralization in fresher systems (Craft 2007). Theoretically, increased salinity accelerates the mineralization of organic matter and the release of NH_4^+ (Noe et al. 2013) as thermodynamically favorable metabolic pathways, such as Fe(III) or SO_4^{2-} reduction (discussed above), increase in importance. However, this expectation is not always met, and the literature includes reports of salinity increasing (Weston et al. 2006, Craft 2007), decreasing (Roache et al. 2006), or having no effect (Ibañez et al. 1999) on organic matter decomposition in wetlands (See *Carbon metabolism*, below).

While mineralization internally regenerates N, microbial N_2 fixation introduces new N to the system by converting atmospheric N_2 to organic N. To our knowledge, no direct assessment of N_2 fixation in response to salinization has been made. Dinitrogen fixation is generally controlled by nutrient status, not by salinity (Howarth et al. 1988), and rates of N_2 fixation are much lower than internal recycling of N (Neubauer et al. 2005a). We thus expect that changes in N_2 fixation will not be a major contributor to altered N cycling in response to salinity.

In oxic zones, microbial nitrification converts NH_4^+ to nitrite (NO_2^-) and, finally, to nitrate (NO_3^-). Nitrification decreases with increased exposure to salt water (Rysgaard et al. 1999, Noe et al. 2013) due to sulfide inhibition of nitrifying bacteria (Joye and Hollibaugh 1995). Although Fe can relieve sulfide toxicity as discussed above,

sulfide inhibition of nitrifiers requires only a brief exposure to H_2S , and thus may occur relatively quickly after saltwater intrusion (Joye and Hollibaugh 1995). In the absence of increased sulfide, small increases in salinity (EC from 1,100 to 16,000 $\mu\text{S}/\text{cm}$) can stimulate nitrification in saline soils, but very large increases (EC >16,500 $\mu\text{S}/\text{cm}$) ultimately inhibit nitrification (Pathak and Rao 1998, Ardón et al. 2013).

Nitrification provides oxidized substrate for denitrification, which then converts NO_3^- to N_2 using NO_3^- as the TEA. Along salinity gradients, salinity is negatively correlated with denitrification (Rysgaard et al. 1999, Craft et al. 2009, Giblin et al. 2010). However, the effects of salinization on denitrification rates in freshwater tidal wetlands are not consistent, with studies showing increases, decreases, or no changes in denitrification (Fear et al. 2005, Magalhães et al. 2005, Aelion and Warttinger 2009, 2010, Marton et al. 2012). Sulfide can inhibit denitrification directly by inhibiting the reductase enzymes that catalyze the final steps of denitrification, resulting in incomplete denitrification to NO_2^- , NO , or N_2O (Brunet and Garcia-Gil 1996), or indirectly by reducing NO_3^- availability via the inhibition of nitrification. Increased ionic strength can also interfere with the enzymes associated with denitrification (Glass and Silverstein 1999 as cited in Laverman et al. 2007). Substantial denitrification can also be driven by the use of H_2S and FeS as electron donors, but only in the presence of sufficient NO_3^- thus, if nitrification is inhibited, no increase in denitrification would be expected (Brettar and Rheinheimer 1991, Haaijer et al. 2006, Burgin and Hamilton 2007, Burgin et al. 2012). High Cl^- concentrations can also inhibit both nitrification and denitrification, but microbial communities appear to be able to adapt to high concentrations over time (Hale and Groffman 2006). Overall, there is still considerable uncertainty as to how these key N cycling pathways will respond to salinization (Larsen et al. 2010, Santoro 2010). In addition to determining N availability in local and downstream ecosystems, an enhanced understanding of these processes is necessary if we are to predict global-scale effects of salinity on N cycling. For example, one consequence of H_2S -mediated suppression of denitrification is the potential to generate N_2O , a powerful greenhouse gas. In a recent field study

of greenhouse gas emissions from a salinized freshwater wetland receiving a high load of fertilizer runoff (NO_3^-), N_2O emissions increased 10-fold when SO_4^{2-} was present (Helton et al. 2014).

Dissimilatory nitrate reduction to ammonium (DNRA) converts NO_3^- to NH_4^+ under anaerobic conditions. It may be very important in highly reduced freshwater (Burgin and Hamilton 2007, 2008) and marine sediments (Boon et al. 1986, Tobias and Neubauer 2009), but is not well quantified in freshwater marsh soils (Gardner et al. 1991, Morrissey et al. 2013). Controls on DNRA are not well characterized and rates have been linked inconclusively to C availability (Tiedje 1988, Nogaro and Burgin 2014), S cycling (Brunet and Garcia-Gil 1996, Burgin and Hamilton 2007), and Fe cycling (Weber et al. 2001, 2006), all of which may be affected by salinization. Tiedje (1988) proposed that DNRA is more important in sediments with high organic matter and limited NO_3^- availability, which would occur with the inhibition of nitrification during saltwater intrusion. Giblin et al. (2010) observed a switch from denitrification to DNRA in oligohaline estuarine sediments during periods of summertime saltwater intrusion. Laboratory studies suggest that sulfide inhibition of denitrification drives NO_3^- reduction toward DNRA (Brunet and Garcia-Gil 1996, Senga et al. 2006), effectively shunting NO_3^- reduction from a removal process (denitrification) to an internal transformation (DNRA). High NaCl concentrations have also been proposed to increase NO_3^- reduction via DNRA without concomitant changes in denitrification, although the mechanism for increased overall nitrate reduction is unclear (Laverman et al. 2007). Clarifying the relationships between DNRA, nitrification, and denitrification under salinizing conditions is key to predicting how salinization will alter N cycling in wetlands and what implications this will have for water quality.

Anaerobic ammonium oxidation (anammox), is the process that converts NH_4^+ to N_2 using NO_2^- as an electron acceptor. It is an important contributor to N removal in sewage-treatment facilities, but is poorly studied in natural freshwater wetland systems (Schubert et al. 2006, Zhang et al. 2007). It does seem that in some estuaries and coastal sediments, up to 80% of the

N₂ produced may be anammox-derived (Burgin and Hamilton 2007). Anammox bacteria show high fidelity to specific salinities, indicating they may be salt sensitive, and anammox has been shown to decrease along salinity gradients (Trimmer et al. 2003). Koop-Jakobsen and Giblin (2009) found that, although anammox accounts for a higher proportion of N₂ generation in freshwater wetlands than saltwater wetlands, anammox accounted for less than 3% of total N₂ production, so it is unclear how important this process is in any given location.

Overall, enhanced N mineralization, enhanced DNRA, reduced coupled nitrification-denitrification, and increased NH₄⁺ displacement from ionic effects of saltwater intrusion appear to be the most predictable changes in wetland N cycling. The combined effect of these changes is an increase in free NH₄⁺ in porewater (Ardón et al. 2013), at least on short-term time scales (Weston et al. 2010), which can enhance the potential for eutrophication within wetlands and in downstream ecosystems. Increased N release from wetland sediments may be particularly damaging where salinization also liberates PO₄³⁻ (discussed above), which contributes to algal blooms and hypoxia.

Carbon metabolism (Fig. 3A–i).—Wetland soils contain an estimated 45–70% of all terrestrial C (Mitra et al. 2005) and the accumulation of C in wetland soils can play an important role in reducing greenhouse gas concentrations and mitigating climate change (McLeod et al. 2011). Salinization increases the concentration of terminal electron acceptors (Fe(III), Mn(IV), SO₄²⁻), theoretically stimulating CO₂ production via increased microbial mineralization of organic matter (Chambers et al. 2011, Meiggs and Taillefert 2011, Weston et al. 2011, Marton et al. 2012, Neubauer 2013) and shifting the dominant pathway of anaerobic metabolism from methanogenesis towards higher energy-yielding pathways (e.g., SO₄²⁻ reduction).

The best studied effect of increased salinity on microbial C cycling in freshwater wetlands is the suppression of methanogenesis with the increased availability of SO₄²⁻ (Bartlett et al. 1987, Boon and Mitchell 1995, Weston et al. 2006, Chambers et al. 2011, Poffenbarger et al. 2011, Neubauer 2013, Neubauer et al. 2013). Methanogenesis is a low energy-yielding metabolic

pathway that occurs under a restricted set of physicochemical conditions including anaerobic conditions, ample C substrates, and the absence of alternate metabolic pathways (Ferry 1993, Dalal et al. 2008). Thus, it is not surprising that this pathway responds rapidly to the alteration of water chemistry. Experiments designed to parse out the effects of the ionic (Na⁺, Cl⁻) versus metabolic (SO₄²⁻) components of seawater indicate that SO₄²⁻ has a larger effect on reducing methanogenesis than does NaCl, most likely due to the direct competition between SO₄²⁻ reduction and methanogenesis in S-rich systems (Chambers et al. 2011). In field studies, SO₄²⁻ concentrations as low as 10 mg/L (Helton et al. 2014) have been shown to inhibit methanogenesis, while a meta-analysis along natural salinity gradients identified 4 mM SO₄²⁻ (386 mg/L or the equivalent of 5 psu seawater) as a threshold between low porewater CH₄ concentrations (<25 μM CH₄) and higher levels (up to >500 μM CH₄; Poffenbarger et al. 2011). Nevertheless, Na⁺ and Cl⁻ alone can significantly inhibit methanogenesis in inland systems (Pattnaik et al. 2000, Mishra et al. 2003, Baldwin et al. 2006). These results suggest that methanogen populations along salinity gradients may adapt or migrate in response to salinity exposure, while those experiencing a novel exposure are more sensitive (further considered in *Microbial assemblages* below).

While the overall effect of salinization is generally a decrease in rates of CH₄ production and/or emissions, studies where salinization increases methanogenesis and CH₄ emissions to the atmosphere (Weston et al. 2011) highlight how poorly we understand the complexities of salinization and methane cycling. Methane in wetland soils is subjected to microbial CH₄ oxidation, also called methanotrophy, wherein CH₄ serves as an electron donor paired with an oxidized species (e.g., O₂, NO₃⁻, or SO₄²⁻). Salinization has been found to reduce both aerobic (van der Gon and Neue 1995), and anaerobic methanotrophy, with the aerobic organisms being especially sensitive to salinity (Dalal et al. 2008). Thus, reduced aerobic consumption of CH₄ could result in increased observed CH₄ emissions (e.g., Weston et al. 2011). The anaerobic oxidation of CH₄ has rarely been considered as a mechanism for altered CH₄

emissions in wetland sediments (Smemo and Yavitt 2011). Recently, tidal freshwater sediments have been shown to support high rates of anaerobic CH_4 oxidation coupled to SO_4^{2-} reduction (Segarra et al. 2015) and to Fe(III), Mn(IV), and NO_3^- reduction (Segarra et al. 2013). The interactions between increased SO_4^{2-} reduction, methanogenesis, and CH_4 oxidation (aerobic and anaerobic) are likely to vary with site-specific factors such as soil and water chemistry, O_2 availability, vegetation, and fluctuations in hydrology. However, experiments aimed at parsing out the effects of multiple factors in salinizing soils are rare.

There is not a clear consensus as to how salinization affects total C mineralization (CO_2 plus CH_4); some studies find enhanced mineralization while others did not document interactions between salinization and total C emissions (Hemminga et al. 1991, Setia et al. 2010, Marton et al. 2012). While much emphasis has been placed on terminal metabolic pathways, the decomposition of organic matter may be regulated by other factors including enzymatic hydrolysis, hydrology, and organic matter quality. The enzymatic hydrolysis of complex organic molecules has been proposed to regulate decomposition rates (Boon 1990, Serrano and Boon 1991, Sinsabaugh 1994, Schimel and Weintraub 2003, Allison and Vitousek 2005) and has been tied to rates of C mineralization in wetlands (Sinsabaugh and Findlay 1995, Freeman et al. 1998, Neubauer et al. 2013, Morrissey et al. 2014a). Studies have documented changes in extracellular enzyme activity along estuarine salinity gradients (Cunha et al. 2000, Mulholland et al. 2003, Morrissey et al. 2014b) and in response to experimental salinity manipulations (Jackson and Vallaire 2009, Chambers et al. 2013, Neubauer et al. 2013). Though the mechanisms by which salinization affects enzyme activity are just beginning to be explored, there is clearly a potential for direct effects of ionic strength on enzyme production, stability, and function with implications for the regulation of organic matter mineralization.

Wetland hydrology may mediate how biogeochemical dynamics are affected by salinization. For example, increased inundation reduces the availability of O_2 and lowers soil redox status, preserving organic matter (Neubauer 2013); this

could, to some extent, offset the increased mineralization rates that are expected due to the higher TEA [SO_4^{2-} , Fe(III)] concentrations in saline waters. The periodicity of salinization may also affect C mineralization. Chambers et al. (2011) suggested that pulses of oligohaline water resulted in higher rates of C loss from freshwater wetland soils than would constant freshwater exposure or chronic (persistent) salinization. Evidence to support this suggestion can be found in field studies that show highest rates of CH_4 emission from oligohaline marshes versus freshwater or saline marshes (Poffenbarger et al. 2011, Weston et al. 2014).

Carbon content and organic matter quality can also limit rates of mineralization. Soils containing a higher C content appear to release more C in response to salinization (Marton et al. 2012). Labile organic matter can accelerate rates of SO_4^{2-} reduction (Howarth and Teal 1979) and decomposition in general, while low nutrient availability, or high C:N ratios in organic matter, can inhibit decomposition (Neubauer et al. 2013). In addition to the microbially mediated chemistry described above, other wetland biota are important drivers in the biogeochemical cycling of elements in wetland systems. Macrophytes, diatoms, and other primary producers fix CO_2 from the atmosphere and provide the C for decomposition and the tissue chemistry and growth form of these primary producers will dictate C quality and quantity. Changes in species composition in salinizing wetlands (see *Algae and vascular vegetation*) can further alter mineralization (Fig. 3B). Understanding the effects of salinization on the C emissions (CH_4 and CO_2) and C balance (source or sink) of wetlands will require systematic investigations of multiple steps regulating organic matter breakdown, but will be essential for predicting global climate feedbacks, especially in peat-building freshwater wetlands.

Silica.—Silica biogeochemistry is rarely considered in discussions of wetland biogeochemistry, although wetlands are important contributors to the global Si cycle (Struyf and Conley 2008). The element is important for macrophyte and diatom communities and can play a significant role in coastal eutrophication (Struyf and Conley 2008). In plants, Si structures are important for maintaining leaf shape, physiological processes, her-

bivory and disease resistance, and defense against metal toxicity and salinity (Epstein 2001). Salinization induces Si release from soils (Dove and Elston 1992, Dove 1999, Weston et al. 2006), which may initially aid freshwater vegetation in compensating for salinity stress, although it may also lead to Si export from wetland systems. We have found no studies of Si dynamics in salinizing wetlands, and there is a general paucity of studies of wetland Si cycling (Struyf and Conley 2008).

Conclusions regarding biogeochemistry.—The overall outcome of altered biogeochemistry will depend on water and soil chemistry, the timing and magnitude of salinization, substrate availability, hydrology, and the response of the biotic community. Although uncertainties remain in how wetland biogeochemistry will be affected by salinization, there exists a clear potential for increased N, P, and Si release with implications for internal or downstream eutrophication (depending on the hydrogeomorphic setting), increased C mineralization (and decreased C storage), and increased generation of toxic H₂S with implications for wetland biota (Fig. 3A, B). Changes in biotic communities will, in turn, affect biogeochemical dynamics. Below we discuss the effects of salinization on wetland biota, community composition, ecological interactions, and the complex interaction between wetland biota and biogeochemistry.

Wetland biota

Species richness of most biological groups in freshwaters shows an inverse relationship with salinity (Hammer 1986) and a corresponding decline of aquatic biodiversity has been observed in response to salinization (Hart et al. 1991, Pinder et al. 2004, 2005, Bailey et al. 2006, Lorenz 2014). The response of the biotic community of a wetland may be viewed as hierarchical, with three levels of response: changes in individual organisms, community reordering (or changes in the relative proportion of organisms), and species turnover (immigration and loss). High external concentrations of salts lead to toxic Na⁺ and Cl[−] accumulation in cells and the disruption of the uptake of other essential ions and water, which may ultimately lead to the mortality of freshwater species (Kozłowski 1997). Hydrogen sulfides can also be toxic. The individual traits, ecology,

and life history of any organism determines its tolerance to a given salinity level (Fig. 4) and how it will respond to salinization. Mechanisms to exclude or exude excess ions are metabolically expensive and come at a cost to growth and reproduction. Salinity can also exert ecological impacts in other indirect or non-lethal ways, including changes in species distribution, behavior, reproduction, and feeding. Increased salinity results in changes in community composition and ecosystem structure (Fig. 3B) by altering both the fitness of individuals and the strength of interspecific interactions as different biological groups show different salinity tolerances (Fig. 4). Ultimately, it shifts wetland communities towards species with greater salinity tolerance.

Microbial assemblages.—Due to their extraordinary metabolic diversity, microbes are the principal drivers of nutrient cycling in wetland ecosystems, and salinity is an important determinant of the spatial distribution of bacterial communities (Bouvier and del Giorgio 2002, Casamayor et al. 2002, Crump et al. 2004, Hollister et al. 2010, Asghar et al. 2012). There are three basic, non-mutually exclusive hypotheses regarding how salinization will affect microbial communities: changing composition, changing function, or a combination of both. The first supposes that, since the composition of saline and freshwater microbial communities differs substantially, and they exhibit similar ecological niches filled by metabolically similar organisms, salinization will result in altered community composition without major changes in microbial function as freshwater organisms are replaced by their brackish/saline analogues (Hobbie 1988, Hart et al. 1991, Nielsen et al. 2003). For example, the relative abundance and community composition of N₂-fixers can vary along estuarine salinity gradients (Affourtit et al. 2001). High salinity may favor heterotrophic N₂ fixation by SO₄^{2−}-reducing bacteria (Šantrůčková et al. 2010) while autotrophic N₂-fixing cyanobacteria dominate freshwater systems (Jones 1982). Secondly, microbial populations may display extraordinary plasticity, responding to salinization via variation in substrate affinity, cellular respiration pathways, or other regulatory mechanisms that provide resilience of communities to environmental change via patterns of dormancy, generation time, fast adaptive evolu-

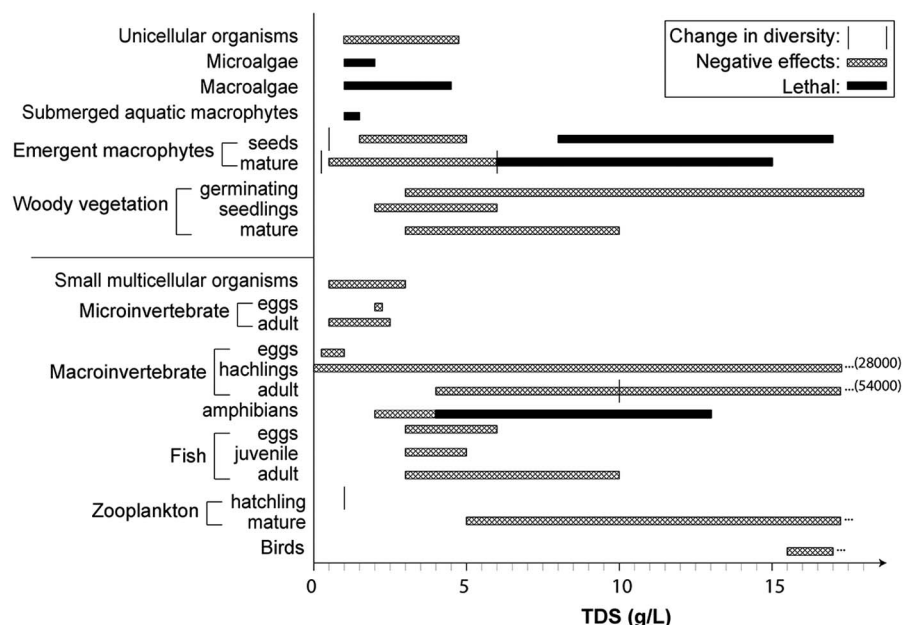


Fig. 4. Generalized salinity thresholds of freshwater wetland biota from literature reviewed in this paper. Where data were available, we present a range, bracketed by lines (| |), or a single threshold (|), where changes in community diversity were observed, a range where negative effects (activity, size, abundance, growth rate, reproduction) occur (crosshatched lines), and a range where mortality occurs (solid black lines). Salinities greater than 15 g/L are presented to the right of the corresponding bar preceded by ellipses. This diagram is derived from a number of primary and secondary data from field observations, mesocosm studies, and traditional laboratory toxicological tests (McKee and Mendelssohn 1989, Hart et al. 1991, Baldwin et al. 1996, Howard and Mendelssohn 2000, James et al. 2003, Nielsen et al. 2003, Kefford et al. 2007).

tion, gene expression, pathway induction, and interspecific interactions without changes in community composition (Edmonds et al. 2009, Nelson et al. 2015). For example, Weston et al. (2006) observed a shift from methanogenesis to SO_4^{2-} reduction in ocean water-amended sediment cores, though this biogeochemical shift was not accompanied by changes in microbial community dominance (Edmonds et al. 2009). Finally, some studies indicate that changes both in microbial community composition and function occur (Jackson and Vallaire 2009). The most consistently observed change is a change in the methanogenic archaea and coincident decrease in CH_4 production (Baldwin et al. 2006).

Prediction of how microbial community composition and function will change is further complicated by site-specific factors. A history of saltwater intrusion can shape the community response (Edmonds et al. 2009, Nelson et al. 2015). Nelson et al. (2015) showed that taxonom-

ic composition remained static in wetlands experiencing first-time salinization; however, those wetlands with a history of salinity exposure developed a reservoir of salinity-adapted communities, which respond quickly to changes in salinity. In inland systems, Hart et al. (1991) reported that cyanobacteria are inhibited by highly variable salinity but may adapt to gradual increases. Observations suggest that Na^+ and Cl^- alone, without a concomitant increase in SO_4^{2-} , can inhibit methanogenesis in inland, but not coastal, systems (Pattnaik et al. 2000, Mishra et al. 2003, Baldwin et al. 2006, Chambers et al. 2011). One explanation of this difference is that methanogens in inland systems are not adapted to periodic saltwater intrusion and thus succumb to direct ionic effects of increased salinity. In contrast, microbes in coastal wetlands are adapted to periodic saltwater intrusion, are able to tolerate high ionic strength and, yet, are still energetically outcompeted by resident sulfate

reducing bacteria when SO_4^{2-} concentrations are elevated. Empirical data from a variety of habitats, a range of scales, and a diversity of microbial functional groups are needed to understand how the structure and function of microbial communities will be altered by salinization (Fig. 4). Furthermore, we lack data on how the composition of wetland microbial communities is tied to their ecological functions, a key gap in our ability to predict how changing community structure will affect ecosystem dynamics.

Algae and vascular vegetation.—There is increasing recognition of the importance of microalgae in wetland food webs (Bunn and Boon 1993, Hart and Lovvorn 2003). There are few studies of the tolerance of freshwater algae to salinity, but it tends to be low (Nielsen et al. 2003 and references therein). Microalgae decrease in both abundance and richness with salinity in inland environments (Blinn 1993, Gell 1997, Blinn and Bailey 2001), though some species have a dormant cyst phase that can remain viable through salinity pulses. Changes in benthic algae have been reported at as little 1 g Cl^-/L (Findlay and Kelly 2011). Diatoms are the subject of considerable research with respect to salinity and brine type and they are widely employed as paleoecological indicators of past salinity due to their high fidelity to specific salinity ranges (Servant-Vildary and Roux 1990, Fritz et al. 1991, Gasse et al. 1997, Gell 1997, Reed 1998). Shifts across taxonomic groups are often reported for macroalgae subsequent to salinization, for example, in the case of charophytes in south-eastern Australia (García 1999). Clear assemblage shifts are evident in the transition from fresh to oligohaline waters, which suggests a diverse flora of salt tolerant taxa, yet how these shifts affect the overall productivity and ecological importance of algae remains to be explored. Algae may be indirectly stimulated by increased light penetration during salinization as a result of increased water clarity, decreased canopy density, and increased nutrient availability (especially Si), however, this is not well studied (Davis et al. 2003, 2010).

Freshwater vascular communities are more diverse and heterogeneous than their saline counterparts, sometimes containing an order of magnitude more species. Reduced primary productivity and biodiversity is one of the clearest

effects of salinization on vascular plant communities (Odum 1988, Hart et al. 1991, James et al. 2003, Nielsen et al. 2003). Physiological mechanisms that mitigate salt stress come at a cost of reduced growth, reproduction, and competitive ability (Munns and Tester 2008). Emergent and submerged freshwater vegetation may exhibit various sub-lethal responses to ionic stress, including a reduction in flowering, height, biomass, leaf proliferation, and size while displaying increased leaf burn, wilting, and chlorosis (James and Hart 1993).

Freshwater vegetation may be resilient to acute pulses of low salinity water (Goodman et al. 2010, Hopfensperger et al. 2014). Hopfensperger et al. (2014) found that repeated annual exposure to low levels of salinity (2–7 psu), experienced only during the growing season, did not significantly alter species distributions at a field site in North Carolina (USA) while Sharpe and Baldwin (2012) showed that prolonged exposure to 12 psu water altered plant communities in a single growing season. McKee and Mendelssohn (1989) suggested that gentle increases in salinity were tolerated, while abrupt increases caused dieback. Flynn et al. (1995) showed that, in coastal Louisiana (USA) marshes, salinity induced aboveground mortality and, while vegetation recovered from short pulses, seeds and rhizomes did not re-grow after longer flooding times with high salinity which resulted in low redox and high H_2S concentrations.

In systems with increased SO_4^{2-} , H_2S (and HS^- at increasing pH) acts as a phytotoxin, reducing nutrient uptake, and inhibiting root respiration (Fig. 3B; King et al. 1982, Lamers et al. 2013). Concentrations as low as 10–20 $\mu\text{mol H}_2\text{S}/\text{L}$ can be toxic. Typically, marine herbaceous species (*Spartina* species, seagrasses) and mangroves are more tolerant to H_2S than freshwater species, but sensitivity may vary among freshwater and brackish water species (Lamers et al. 2013). Whether or not salinization will lead to H_2S toxicity largely depends on the availability of Fe in the soil (Portnoy and Giblin 1997b, van der Welle et al. 2006, Lamers et al. 2013). Wetland vegetation experiencing ionic stress often produces N-rich compatible solutes (e.g., proline) to balance osmotic potentials, increasing N demand and tissue N (Cain and Boon 1987, Larsen et al. 2010). High concentrations of H_2S , however, may

stymie this response by inhibiting N uptake. Portnoy and Giblin (1997a) report that an abundance of inorganic N, such as increased NH_4^+ , in salinizing sites could also help overcome H_2S inhibition. However, at high concentrations, NH_4^+ can become toxic to macrophytes (Clarke and Baldwin 2002). Clearly, the interaction between H_2S toxicity and inorganic N is complex and warrants further investigation, especially as eutrophication is a growing concern for wetland systems (Larsen et al. 2010).

Chronic salinization results in the replacement of freshwater species by brackish, or salt-tolerant, vegetation (Hart et al. 1991, James et al. 2003, Nielsen et al. 2003). In Australian freshwater systems, reduced productivity and decreased botanical diversity occurred with chronic increases in salinity to ~ 1 g TDS/L; at ~ 4 g TDS/L marked changes in vegetation can be expected (Fig. 4; Hart et al. 1990). Recently, others have found similar tolerances to chronic salinities, between 1 g TDS/L and 6 g TDS/L, for freshwater wetland communities in inland and coastal settings (Spalding and Hester 2007, Sutter et al. 2014). In Australian wetlands, salinities between 0.6–0.9 g TDS/L are predicted to reduce species richness of aquatic macrophytes by 30–50% and at 3.5 g TDS/L reductions may exceed 60% (Brock et al. 2005).

Herbaceous freshwater wetlands contain substantial seed banks in the sediments, with high proportions of annual species (Odum 1988). Decreased germination and reduced seedling survival begins at TDS levels less than 1 g TDS/L (Fig. 4; Hart et al. 1990, 1991). Sharpe and Baldwin (2012) observed that seasonal low-salinity saltwater intrusion into estuarine wetlands in the Nanticoke River (Maryland, USA) dispersed brackish species upstream, increasing diversity where fresh and brackish species coexisted. However, seed propagule dispersion may be limited in isolated depressional wetlands causing them to experience major declines in diversity (Leibowitz 2003). Clonal reproduction is favored over sexual reproduction in salinized environments (Robinson et al. 2006, 2012). Salinization may promote exotic species invasion by altering species abundance and fitness (Cramer et al. 2004, Rahel and Olden 2008), and, indeed, some freshwater exotics have been shown to have more favorable mechanisms for

tolerating salinity or saline pulses, giving them a competitive advantage over their native counterparts (Pathikonda et al. 2009, Thouvenot et al. 2012). For instance, in coastal wetlands in southeastern Australia, the relatively salt-tolerant swamp paperbark (*Melaleuca ericifolia*) can persist via clonal growth for decades at salinities exceeding 20 g TDS/L (Boon et al. 2008, Raulings et al. 2010), contributing to its invasiveness.

Woody freshwater species are often particularly sensitive to salinity, and, while they may survive acute salt pulses (>18 g TDS/L for short periods), chronic salinization leads to complete mortality and irreversible transition to herbaceous marsh (Conner et al. 1997, Krauss et al. 2007). Relatively low salinity (3–10 g TDS/L; Fig. 4) can result in defoliation, branch mortality, epicormic branching, stunted growth, and reduced sexual reproduction, ultimately altering species dominance, biomass, and diversity (Brinson et al. 1985, Conner et al. 1997, Robinson et al. 2006, Desantis et al. 2007, Krauss and Duberstein 2010, Salter et al. 2010a, b, Robinson et al. 2012). Salinity exposure just a few times a year in Florida Gulf Coast (USA) tidal freshwater forests reduced diversity from > 20 species to stands of cabbage palm (*Sabal palmetto*) and southern red cedar (*Juniperus virginiana*; Desantis et al. 2007). Chronic salinization, resulting in the extirpation of large trees, has been reported widely for black box (*Eucalyptus largiflorens*) and river red gum (*Eucalyptus camaldulensis*) on the floodplains of rivers across inland Australia (Mac Nally et al. 2011), and for the floodplain cypress-gum swamps (*Taxodium* and *Nyssa* species) of southeast United States (Conner et al. 2007).

Life history and morphological adaptations may induce resilience to salinity in woody species. Due to their deep root structure, trees can access groundwater to avoid salinity stress (Krauss and Duberstein 2010) and clonal species, such as swamp paperbark, can persist under highly saline conditions (Montagna et al. 2002, Boon et al. 2008, Raulings et al. 2010, 2011). There is some indication that more salt tolerant genetic strains of certain woody species, including baldcypress (*Taxodium distichum*) and species of *Eucalyptus* and *Melaleuca*, could maintain forest diversity in the face of mild salinization (Niknam and McComb 2000, Krauss et al. 2007). Although freshwater woody species will likely be replaced

by salinity-tolerant woody and herbaceous species, this salinity-induced transition will reduce many important services provided by forested wetlands, including C storage and habitat provision as freshwater forested wetlands tend to have greater structural complexity than their saline counterparts (Lugo et al. 1988). Salinization may also favor the invasion of salt-tolerant woody species in North America, including Chinese tallow (*Triadica sebifera*), salt-cedar (*Tamarix chinensis*), and paperbark (LaRoche and Ferriter 1992, Rahel and Olden 2008, Howard 2012).

Altered hydrology may also play a role in mitigating or aggravating salinity stress, but no clear pattern has been established (Flynn et al. 1995, Spalding and Hester 2007, Sharpe and Baldwin 2012). Depending on a wetland's elevation relative to mean high tide, moderate increases in inundation can either stimulate or depress rates of primary production (Morris et al. 2002, Kirwan et al. 2010). Increased inundation reduces seedling growth and recruitment (McKee and Mendelssohn 1989, Baldwin et al. 2010). Individual species respond differently to the combined effects of waterlogging and salinity (Spalding and Hester 2007); for instance, perennials are more tolerant to increased inundation (Baldwin et al. 2001), whereas woody species are less tolerant (Conner et al. 1997).

Together, these studies suggest that individual stress and community reordering can occur at moderate salinities. However, at high salinities, freshwater species are replaced with brackish communities, resulting in lower diversity and productivity. Salinity-induced shifts in plant community composition may vary depending on the landscape position of the wetland and the mechanism of salinization, with additional complexities such as water chemistry (N, H₂S) and altered hydrology (Fig. 3B). Recruitment of salt-tolerant macrophytes is not guaranteed, as it requires that these species are present in the local seedbanks or that viable propagules can disperse from adjacent saline ecosystems (Fig. 3B).

Changes in plant communities can enforce important feedbacks that affect the biogeochemistry. Organic matter mineralization is a key ecosystem process regulating the regeneration and availability of nutrients, C sequestration, and soil integrity of a wetland system (Reddy and DeLaune 2008). Given that salinity can alter the

production of organic matter, activity and composition of microbial communities, physicochemical environment, cation exchange sites, and nutrient availability, forecasting the consequences of increased salinization on organic matter decomposition in wetlands will require integrating biogeochemical dynamics with plant community dynamics. In one of the few long-term studies, Neubauer (2013) showed that soil CO₂ production increased in response to a short-term salinity pulse but declined over time in response to long-term (3.5 years) salinity exposure. Neubauer et al. (2013) attributed this to long-term indirect feedbacks that affected the composition of soil organic matter (e.g., higher C:N ratio) and were potentially driven by changes in plant productivity and species composition. Alternatively, Hopfensperger et al. (2014) saw that saltwater intrusion during the growing season (peak salinities 2–7 psu) did not influence the distribution of plants during the study period, potentially due to the short duration, low salinity, and prevalence of Fe to buffer H₂S toxicity. They did observe that the presence of graminoid plants was highly correlated with increased SO₄²⁻ reduction, increased Fe oxide plaque development on roots, and reduced CH₄ production upon saltwater intrusion, potentially due to increased delivery of O₂ to the rhizosphere via radial oxygen loss. This illustrates the temporal variability in the response to salinization between different ecosystem components and highlights the need to understand the coupling between plant and microbial processes.

Not only will changes in vegetative communities interact with subsurface biogeochemistry, they will also interact with invertebrate and vertebrate consumers who utilize vegetative structures for food and refuge. Changes in the productivity and quality of plant tissue (C:N, Si) will impact rates of herbivory and the nutrient content of herbivores, with ramifications up the food web. In one of the few studies of the effects of salinity on herbivore grazing, Geddes and Mopper (2006) found that deer grazing on the reproductive structures of Dixie iris (*Iris hexagona*) was higher in freshwater marshes following saltwater intrusion and attributed this to both the death of preferred food plants, which shifted grazing to the iris, and to an increase in palatability of the iris. This potentially important

indirect feedback between community composition, plant tissue chemistry, and herbivory has rarely been included in discussions of wetland salinization.

Invertebrates and vertebrates.—Invertebrates are an important part of the wetland food web base, and salinity has major implications for invertebrate diversity and community structure. Many studies have found freshwater invertebrate species richness to decrease with an increase in salinity (Cale et al. 2004, Waterkeyn et al. 2008, Stewart et al. 2009). Pinder et al. (2005) identified 4.1 g TDS/L as the threshold above which species richness declined in isolated wetlands in the Australian wheatbelt. Osmoregulatory functions of freshwater invertebrates fail around 9 g TDS/L, but sub-lethal effects including reduced growth, stunted reproduction, and behavior change have been observed at salinities as low as 0.8 g TDS/L (Fig. 4; James et al. 2003). Small, sessile organisms, like insect larvae and mollusk recruits, are differentially impacted by increased salinity and invertebrate hatchlings are generally restricted to salinities below maximum adult salinity tolerances (Hart et al. 1991). Waterkeyn et al. (2008) found rare freshwater invertebrate species to be more sensitive to salt disturbances than abundant species in the Camargue wetlands of southern France. As in the case of vegetation, replacement of invertebrates by salt-tolerant taxa may be dispersion-limited in isolated wetlands. Pinder et al. (2004), in a survey of 223 Australian inland wetlands, showed that while there is evidence of the colonization of salinized wetlands by salt tolerant invertebrate species, salinized sites are more homogenous than natural saline wetlands. In riverine and estuarine systems, connectivity and water exchange should facilitate replacement by downstream taxa. Salinity may interact with hydrology to impact wetland communities. Bolduc and Afton (2003) documented a strong effect of salinity on oligochaetes and nematodes, and found that flooding and anoxia reduced their ability to compensate for salinity stress.

Similar to invertebrates, the embryonic and juvenile life stages of vertebrates are far more sensitive to elevated salinity than are their adult counterparts (Hart et al. 1990, 1991, James et al. 2003, Kefford et al. 2012). Anurans are extremely sensitive due to their permeable skin, with

similar salinity tolerance to many invertebrates. Direct effects of salinity include developmental anomalies, egg and larvae mortality, reduced larval growth rates, and altered larval behavior (Petranka and Francis 2013). Tadpoles living in saltwater have reduced survival even when the salinity is within the natural tolerance range of adults (Rios-Lopez 2008). Fish species seem to be more tolerant; adult fish species found in Australian freshwater wetlands can survive salinities of between 7 and 13 g TDS/L, even in early life stages; the growth optimum for juveniles is 3–5 g TDS/L (James et al. 2003, Nielsen et al. 2003). Although water birds are highly motile, breeding is often confined to less-saline waters, around 15 g TDS/L (Goodsell 1990, Halse et al. 1993, Nielsen et al. 2003). As early as the 1970s, there was an appreciable reduction in water bird nesting habitat in the South-West Australian Wheat Belt concomitant with widespread salinization. In the early 1990s, a large colony of white ibises (*Eudocimus albus*) left coastal South Carolina (USA) in the years following Hurricane Hugo, not because of the direct effects of the storm on the birds but because the storm surge sent saline water into freshwater wetlands, causing significant negative effects on crayfish populations (*Procambarus* spp.), the primary food source for white ibis nestlings (Michener et al. 1997). In some cases, although saline waters may be prohibitive to breeding, they may still be utilized by transient species, especially birds, for feeding and loafing (Halse et al. 2003).

As we progress up the food chain in our discussion, there is increased emphasis on indirect effects on the health and survival of wetland biota. The resilience of a community will depend on how salinization impacts food resources and the availability of refugia. Even mobile fauna in relatively open systems (e.g., estuaries or floodplains) may suffer declines as salinization reduces habitat and results in unforeseen changes in food web and community structure (James et al. 2003). For salt-tolerant organisms occupying higher trophic levels, a lack of nursery habitat for prey fish, exposure to higher than optimum metabolic salinities, and low primary productivity may drive declines in abundance and biomass. High salinity decreases primary productivity with the potential for

cascading effects at higher trophic levels (Lorenz 2014), and high variations in salinity result in inferior diet (Ley et al. 1994). Petranka and Francis (2013) concluded that spotted salamander larvae were more salt tolerant than their invertebrate prey and that, at salt concentrations of 1 g/L, salamander growth was inhibited indirectly via poor prey quality. Freshwater diversions in Taylor Slough (Florida, USA) have been implicated in major vertebrate declines since 1984, driven by declines in prey quality and quantity (Lorenz 2014). Similarly, in the Coorong (Murray River, South Australia), increasing salinity is associated with the displacement of migratory birds from historically freshwater areas by endemic banded stilt (*Cladorhynchus leucocephalus*), which prey upon brine shrimp (*Parartemia* sp.; Kingsford et al. 2011). However, at least one study concluded that, although shifts in the base of foodweb are observed at different salinities, salinity effects on invertebrate communities are less important than the cost of osmoregulation to avian consumers (Wollheim and Lovvorn 1995).

Conclusions regarding wetland biota.—Species turnover and habitat shifts will be determined by a wide range of biotic and environmental factors, including species-level tolerances, community interactions, and landscape-level considerations. Salt exposure constitutes a constant refining of the species pool based on salinity tolerance, morphology, phenology, motility, and life-history. Increased salinity will favor colonization by salt-tolerant species, but species replacement will depend on the incidence and dispersal ability of saline analogues across salinizing landscapes. For a given wetland, its hydrogeomorphic character, history, and proximity to saline ecosystems will determine the pool of potential re-colonizers (Nielsen and Brock 2009). Isolated inland systems, especially those lacking surface water connectivity, are especially at risk due to their limited potential for colonization by salt tolerant species. Unfortunately, those systems are often unique habitat with high local endemism (Nielsen and Brock 2009). The rate, periodicity, and seasonality of salinization will also affect species turnover and recolonization (Nielsen et al. 2003, Brock et al. 2005, Nielsen and Brock 2009). Species that have broad salinity tolerance at an adult life stage may

still be affected by changes in timing and duration of salinization, likewise highly mobile species may still experience declines in available food and refugia quality across salinizing landscapes. Because different groups and individual organisms display a wide range of salinity tolerance (Fig. 4), there is a high potential for the disruption of existing ecological interactions, so called decoupling, due to altered abundance, activity, reproductive success, or extirpation.

SALINIZED LANDSCAPES

There have been few attempts to examine how salinization affects landscapes as a whole. In general, salinization induced by any mechanism will occur at large spatial scales, shifting the distribution of species and processes across entire landscapes. Using model simulations from the Intergovernmental Panel on Climate Change (IPCC), Craft et al. (2009) predicted that brackish marsh coverage in coastal Georgia (USA) would increase by 10–45% given an increase in sea level of 52–82 cm, respectively. This expanded brackish marsh is a direct result of freshwater marsh salinization. Craft et al. (2009) concluded that, although this transition would shift species distribution and reduce the denitrification potential from these marshes, it would not affect standing biomass or N accumulation in soils. Brackish marshes may be expected to migrate inland as salinity intrudes into freshwater reaches, although this modeling exercise relied on extrapolating existing estuarine patterns to the salinization process. Documenting cases of wetland salinization is the first step in assessing the extent of this problem (see *The global extent of salinization*); utilizing geophysical and hydrological models to predict salinization will be important in predicting salinization in the future.

Many modeling studies, including Craft et al. (2009), assume a gradual transition from freshwater to brackish communities without the potential for lags or critical thresholds that may shift ecosystems to open water before vegetation transitions can occur. Increased salinity has been associated with the conversion of coastal marshes and wetlands to open water (Nyman et al. 1993, DeLaune et al. 1994). In Mississippi River Delta (USA) wetlands, a positive feedback was observed whereby saltwater-induced decomposi-

tion resulted in subsidence, and increased flooding caused more plant mortality, further accelerating peat collapse, erosion, and marsh loss (Delaune et al. 1994). It is estimated that Louisiana (USA) has lost $4,920 \text{ km}^2 \text{ yr}^{-1}$ of wetlands to open ocean due to increased flooding and salinity (Barras et al. 1994, 2003). Salinization, even when occurring at a slow pace, may trigger catastrophic regime shifts in wetland ecosystems resulting in a transition to an alternative stable state (Scheffer and Carpenter 2003, Sim et al. 2006, Davis et al. 2010). In the case of the Mississippi River Delta, salinity-induced marsh failure resulted in the collapse of marshes into open water before a transition to salinity-tolerant vegetation could occur.

As with other alternate stable-state examples, positive feedback loops tend to reinforce the new state and hysteresis makes it difficult to reinstate the original condition, especially in concert with other disturbances such as rising sea level, marsh channelization, and decreased sediment supply. In tidal freshwater forests in the United States, salinization-driven death of trees results in the conversion to herbaceous marsh; often, this change is irreversible as the collapse of woody root structures results in subsidence, increased inundation, and inhibition of seedling growth (Williams et al. 2003, Desantis et al. 2007, Krauss et al. 2007). Similarly, the onset of secondary salinization in inland systems in Australia can decrease the resilience of macrophyte-dominated systems over time and drive them toward benthic, microbial-mat dominated systems (Strehlow et al. 2005, Sim et al. 2006).

Whereas shifts between freshwater and brackish macrophyte-dominance may have little consequence for overall ecosystem structure and function (Craft et al. 2009), shifts between forested and herbaceous wetlands, or between herbaceous wetland and open-water, greatly alter ecosystem structure and function. These state transitions can cause an associated loss of habitat, decreased biomass, changes in ecosystem C storage, shading of fringing aquatic environments (with implications for water temperature and light regimes), and other ecosystem-wide ramifications. The overall consequence, then, is a homogenization of the landscape and a large-scale reduction of the ecosystem services provided by wetlands with consequences for water

quality, biodiversity, and climate forcing. Understanding these lags and thresholds will require long-term monitoring and manipulative experimentation that can inform predictive models.

Salinization is often associated with changes in wetland geomorphology due to altered mineral and organic sediment dynamics. Unfortunately, it is particularly difficult to anticipate how salinization will affect wetland geomorphology because of the multitude of interacting factors and the spatial scale of change. In areas with large tidal ranges, and relatively smaller elevation differences (e.g., Coastal plain of Atlantic coast, USA and northern and western Australia), SLR and saltwater intrusion have resulted in the extension and elaboration of tidal creek networks. For example, in the Mary River in northern Australia, Knighton et al. (1991) observed extensive headward expansion and tributary development at rates up to 0.5 km yr^{-1} , resulting in the expansion of saline tidal creeks into over 17,000 ha of freshwater marsh. Likewise, in southeastern Australia, the loss of reed beds has contributed to the erosion of geomorphologically significant silt jetties in the Gippsland Lakes (Bird 1961, 1962, 1970, Bird and Rosengren 1971).

The ability of coastal marshes to keep up with SLR will depend on the enhanced organic matter accretion and accelerated sediment deposition (Kirwan et al. 2010). Freshwater wetlands tend to rely heavily on organic inputs to maintain elevation (Neubauer 2008), and organic matter accretion typically decreases following salinization (Fig. 3B; Spalding and Hester 2007). In organic soils, increased decomposition (see *Carbon metabolism*) and reduced root biomass may further accelerate subsidence, increasing rates of flooding with feedbacks to plant communities (Mac Nally et al. 2011, Pittock and Finlayson 2011). Salinization may also increase sedimentation (*Ionic change*, above) as the peak of fluvial sediment trapping often occurs at the head of the salt wedge when saltwater intrudes upriver (Meiggs and Taillefert 2011, de Nijs and Pietrzak 2012). The net outcome will depend on soil composition (mineral versus organic) and mineral sediment loads, among myriad other factors. Understanding the geomorphic consequences of wetland salinization in coastal wetlands will be key in predicting how flood protection services

of coastal wetlands will change as more than one-third of the global population lives in the coastal zone (McGranahan et al. 2007).

OVERALL CONCLUSIONS

Instances of wetland salinization will increase in frequency and severity around the globe as a result of climate change and increased human alteration of the hydrologic cycle. Increased wetland salinity alters the fundamental physico-chemical nature of the soil-water environment, induces physiological stress in wetland biota and, ultimately, results in large shifts in wetland communities and their associated ecosystem functions. Although the specific consequences of salinization will vary on a case-by-case basis, we have identified six general characteristics that shape wetland ecosystem response to salinization. (1) The geomorphic position of a wetland will influence wetland hydrology and its effect on the (2) timing and magnitude of salinization as well as the (3) origin and ionic composition of dissolved salts. Salinity in inland systems will differ from coastal wetlands in both ionic strength and composition, especially SO_4^{2-} concentration (Table 1). (4) The mineral content of a wetland soil, particularly Fe, will influence both how susceptible wetland soils are to subsidence and C loss via increased decomposition and the potential of H_2S toxicity. Finally, the replacement potential of salt-tolerant species will be mediated by (5) historical patterns of salinity within a particular wetland that shape the current community composition and presence of salt-tolerant propagules and (6) the proximity and connectivity of a wetland to other saline systems. Colonization potential is high in connected systems like estuarine wetlands, or inland wetlands in landscapes with a history of salinity fluctuations, but will be low in geographically isolated wetlands experiencing salinity for the first time.

Two factors will make wetland salinization an unusually complex process to manage. First, as this review has shown, salinization involves complex and often unpredictable interactions between multiple ecosystem components, acting over a variety of spatial and temporal scales (Fig. 3B). Although we understand the response of many individual ecosystem components to salinization,

it is their interactions that will determine the eventual state of a wetland ecosystem and whether or not ecosystem transition is reversible. Complex non-linear feedbacks between ecosystem components are understudied, but knowledge of these feedbacks will be essential in predicting the outcome of salinization. In some cases, these feedbacks may exacerbate (positive feedback) or ameliorate (negative feedback) the impacts of salinization. Using the extensive data provided by decades of salinization research, we hypothesized likely outcomes for wetland ecosystems undergoing salinization that includes potential feedbacks between ecosystem components at many scales (Fig. 3B). Many of these feedbacks will only be apparent in plot-scale manipulations or field-scale observational studies, which remain rare.

Secondly, salinization rarely occurs as an isolated perturbation, but instead is associated with other concomitant changes. Increased salinities will interact with other global changes including altered hydrologic regimes, increased temperatures, and increased N loads (Larsen et al. 2010, Mac Nally et al. 2011). Wetland salinization takes place within a much wider milieu of social, economic, and political considerations; its resolution, therefore, can take place only within a similarly complex set of management decisions and policy directions, informed by high-quality and relevant science. As Nielsen and Brock (2009) noted in their review of secondary salinization in Australia, the preservation of freshwater wetlands will likely require increasing human intervention and management of the entire landscape.

The first step in preserving freshwater wetlands will be the identification of wetlands currently undergoing salinization and those at risk for salinization in the future. To that end we have provided an overview of the causes of salinization. While preventing salinization at local scales via controlling point-source discharges or drawing down saline groundwater may be feasible, landscape scale salinization and salinization associated with global change will be more difficult to control. Where the salinization of wetland ecosystems is unavoidable, these systems may also prove to be a fertile testing ground for broader ecological theories including (but not limited to): alternative stable states and

tipping points, trophic cascades, disturbance-recovery, and the role of historical events and landscape context in driving community response to disturbance. Due to the complex nature of wetland systems, we encourage a greater research emphasis on whole-ecosystem and landscape-scale studies.

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